WHY MONOGAMY? COMPARING HOUSE WREN SOCIAL MATING SYSTEMS IN TWO HEMISPHERES

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Paulo E. Llambias

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WHY MONOGAMY? COMPARING HOUSE WREN BREEDING SYSTEMS IN TWO HEMISPHERES

Paulo E Llambias, Ph. D.

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The evolutionary basis for strict monogamy remains unclear. It has been suggested that monogamy might be maintained in cases where: 1) female fertility is synchronous within the population, 2) resources are evenly distributed so that male territories are of similar quality, 3) male-male competition prevents males from acquiring more than one female or 4) female-female aggression prevents additional females from settling in monogamous territories. During 2003-2007, I carried out research on the social mating system and parental behavior of a migratory population of northern house wren (*Troglodytes aedon aedon*) and a resident population of southern house wren (*Troglodytes aedon bonariae*) breeding in nest-boxes in the U.S. and Argentina, respectively. Northern house wren females bred more synchronously than southern house wrens, so synchrony does not explain the higher prevalence of polygyny in the north. The addition of nest-boxes to increase territory quality of occupied territories did not stimulate polygyny in southern house wrens. Only removal of territorial males and floaters increased the polygyny rate in the southern house wren, suggesting intense competition for breeding territories. Strong competition for breeding sites could be a consequence of higher adult survival in the south leading to lack of enough territories to breed in relation to population density. Indeed, southern house wrens bred in smaller territories than northern house wrens. Northern and southern house wrens visited a caged female close to the primary and secondary boxes in similar proportions. Both were aggressive to the caged female close to the primary nest-box, but a higher proportion of southern house wren females were aggressive when the cage was installed close to the secondary box. Female aggression in the southern house wren might be related to the smaller size of territories. Indeed,

southern house wren polygynous males' territories were of similar size to northern house wren territories, but monogamous southern house wren territories were smaller than northern house wren territories. I suggest that southern house wren males are monogamous because they are unable to monopolize more than one female. This pattern seems to be dominated by two processes: male habitat saturation and female territoriality.

BIOGRAPHICAL SKETCH

Paulo was born in 1970 in Bahía Blanca, Argentina. He spent most of his vacations in the outdoors since his parents were geologists at the University of Bahía Blanca. As he grew up, he developed a passion for mountains and natural history, and when he finished high school in Buenos Aires he decided he wanted to be a biologist.

He attended the University of Buenos Aires, realizing that his major interest in biology was in the area of behavioral ecology. He started working in animal behavior in 1994, when he volunteered as a field assistant for Prof. Fabian Gabelli to study song dialects in sedge wrens, in collaboration with Dr. Donald Kroodsma from the University of Massachusetts. While in the field, Paulo acquired the tools necessary for the study of avian biology, and back at the laboratory he learned how to interpret and analyze data. He was surprised to see how ecological variables can affect singing behavior and started wondering how those same variables might affect mating systems. During his years at the University he climbed with Marcos Tanke, an undergraduate student at the same university. Together they ascended Lanin (3747m), Tronador (3187m) and El Plata (6300m).

In 1997, Paulo joined Dr. Thomas Martin's field crew in northern Argentina to collect data on breeding biology and life histories of tropical passerines. This was the beginning of a long friendship with Tom and an excellent opportunity to learn new field techniques on breeding biology of birds and the whole scientific process. Paulo worked with Tom in the mountain forests of Argentina, Ecuador, and Venezuela and in temperate forest in Arizona. While in Ecuador, he did not miss the opportunity to climb, and he ascended Cotopaxi (5898m) in 12 hours during a break in the field work.

In 1998, Paulo started the research for his honor's thesis to complete his degree

at the University of Buenos Aires under the supervision of Dr. Juan Carlos Reboreda. During two breeding seasons, he worked in the field to understand the effects of Shiny Cowbird parasitism on the breeding success of the Rufous-bellied Thrush. In 1999, Paulo graduated after defending his honor's thesis, which was awarded the maximum score.

In 2002, Paulo was accepted as a graduate student in the Department of Ecology and Evolutionary Biology at Cornell University, where he completed a Master's degree on mate retention in tree swallows and began a study of how ecological variables affect social mating systems in house wrens, to be the basis for his Doctoral dissertation. While living in the US, Paulo continued with his outdoor activities, which included solo treks in the Alaska Range and the Continental Ice Sheet in Patagonia and cross-country ski, water-fall ice and rock climbing with his office-mate, house-mate and friend Mike Booth. At present Paulo is applying for a research position in Argentina to continue his research on mating systems and training for ascending Aconcagua (6962m) with Marcos Tanke.

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CHAPTER 1

MATING SYSTEMS, SPATIAL DISTRIBUTION, AND LIFE-HISTORY TRAITS OF NORTHERN AND SOUTEHRN HOUSE WRENS

Paulo E. Llambias, Marian Carro, Kathleen LaBarbera and Irby J. Lovette.

Abstract

Northern and southern temperate passerines differ in life-history traits, with southern species generally characterized by higher adult and juvenile survival, smaller clutches, and longer incubation and nestling periods. High adult survival is often associated with low rates of social and genetic polygamy, hence monogamy is expected to be more common in southern temperate birds. The broad distribution of the house wren (*Troglodytes aedon*) provides a distinctive opportunity to study geographic variation in life-history traits. Here we compare life-history traits and mating systems between a northern and a southern house wren population studied over a five-year period. As predicted, southern house wrens laid smaller clutches (4.86 vs 5.92 eggs), and had longer incubation (15.27 vs 13.89 days) and nestling periods (17.04 vs 15.89 days). Per-nestling parental effort was significantly higher for southern wrens, but the average number of feeding trips to the nest (trips/hour) did not differ significantly. Social polygyny was extremely rare in the southern house wren (1%) while relatively frequent in the northern house wren (18%). A smaller proportion of southern house wren nests contained extra pair young compared to northern house wrens (32% vs. 54%, respectively) but the overall proportion of extra-pair young per brood did not significantly differ. Northern house wren territories were distributed

over a wider variety of habitats and larger area, hence had fewer neighbors, than in the south. We suggest that southern house wren's spatial distribution and non-migratory life-style foster social and genetic monogamy. Although the estimated annual adult survival for southern house wrens was higher than for northern house wrens, the differences were not significant, likely because of small sample sizes and high annual variation in re-sighting and recapture probabilities.

Introduction

Northern and southern temperate birds differ in life-history traits, in particular, southern temperate birds generally lay smaller clutches, and they often have longer incubation and nestling periods, extended parental care, and higher adult and juvenile survival rates (Martin 1996, Geffen and Yom-Tov 2000, Russell 2000). Adult survival seems to be correlated with mating systems; long-lived birds are predominately socially monogamous with low rates of extra-pair paternity, while short-lived birds more often exhibit social polygamy with high rates of extra-pair fertilizations (Bennett and Owens 2002). Hence, we might expect that southern temperate birds will display both social and genetic monogamy. Higher adult survival is thought to be associated with lower parental effort, since the cost of reproduction should reduce future survival (Winkler 1991, Whittingham et al. 1992), so reduced parental effort is also expected in southern temperate birds.

Most research on life-history evolution has focused on differences between the northern temperate and tropical zone, and few papers describe differences between northern and southern temperate-nesting birds (but see Yom-Tov 1994, Russell 2000). Comparisons of life history traits among populations of broadly distributed species are particularly informative, as any differences observed are more likely due to

differences in ecology rather than longer-term differentiation. Only two passerine species, the house wren (*Troglodytes aedon*) and the sedge wren (*Cisthotorus platensis*) have a broad enough distribution to allow interspecific northern-southern temperate comparisons. The objective of this study was to provide comprehensive data on life history traits of northern temperate and southern temperate house wrens based on a five-year study of two color-banded populations.

Methods

Study species

House wrens are small (11-13 g), territorial passerines that breed in natural cavities, holes excavated by other bird species and nest-boxes. House wrens have the broadest distribution of any passerine in the Americas, ranging from Canada to Tierra del Fuego. These populations are most often grouped taxonomically as a single species (*Troglodytes aedon*, Remsen et al. 2009), although it has also been proposed (Brumfield and Caparella 1996) that these population should be divided into three species: the northern house wren (*Troglodytes aedon*), the brown-throated house wren (*T. brunneicollis*), and the southern house wren (*T. musculus*). In addition to morphological traits that differ among house wren populations, they also exhibit substantial behavior variations. For example, northern house wrens are mainly migratory, between 15-35% have been reported to be polygynous breeders, and extra-pair fertilizations are frequent (Johnson 1998). Southern house wrens are mainly sedentary and social polygyny is relatively rare (Brewer 2001, Llambías and Fernández 2009).

Study sites

During October-January, 2003-2007, we studied a resident population of southern house wrens breeding in nest-boxes in deciduous costal woodlands at a private cattle ranch, "Los Zorzales" (36°26'S, 56° 25'W), near General Lavalle, Buenos Aires Province, Argentina. Before first erecting nest-boxes, we mapped male territories using song playback to stimulate singing behavior. We observed each male's movements inside the territory to define the territory's core, and agonistic interactions with neighbors to define its borders. Boxes were erected 15-30 days before the first egg was laid in the population, and were added to additional plots during the study period. In 2003, we erected two boxes in each of 47 territories in three forest fragments (total area = 4.1 ha), each fragment separated by 50m of pasture. In 2004, we added two nest-boxes per territory to 12 territories of mated pairs in 5 additional woodlot patches (total area = 5 ha), each separated by 100m of pasture. We added two boxes to the rest of the territories in 2006. All boxes were attached with wire to main branches of trees, 1.7 - 2 m off the ground. After wrens had started building a nest inside the nest-box we reduced the entrance hole diameter from 38 to 27 mm to preclude the entry of shiny cowbird (*Molothrus bonariensis*) brood parasites.

During May-August, 2003-2008, we carried out research on a migratory population of northern house wren at Cornell Experimental ponds Units 1 and 2 (42° 28'N, 76° 29'W), near Ithaca, New York, USA. Prior to the breeding season, we erected nest-boxes on greased poles, 1.5m high, and 25-50m apart (2-3 boxes per territory, 68 boxes erected at Unit 1 in 2003 and 60 at Unit 2 in 2004).

Boxes in both populations were newly constructed from wood, with dimensions of 30.5 x 16.5 x 12.7cm and an entrance hole located in the front. In both

populations the entrance hole diameter was 38mm, but in Argentina was reduced to 27mm once the wrens started breeding.

Field procedures

At both study sites we color-banded 77-88% of the breeding adults. We trapped wrens in the nest-boxes or with mist nets. To assess rates of extra-pair fertilizations, we collected blood samples from the brachial vein from adults and nestlings of 30 southern and 82 northern house wren nests during 2003-2004. The blood samples (50-100 uL) were stored in lysis buffer (0.1 M Tris, pH 8.0, 0.1 M. EDTA, 10 mM NaCl, 0.5% SDS, White and Densmore 1992)

We checked nest-boxes every two-three days. When possible, we checked the nests with eggs close to hatching or nestlings close to fledging every day to record exact hatching and fledgling day. For each nest we recorded lay date, clutch size (number of eggs laid), brood size (number of nestlings hatched) and fledging number (number of nestling fledged). We classified nests as "pecked" by another house wren when eggs had small holes pecked on them or we found dead nestlings close to or inside the nest cup with marks of pecking on the head. We classified a nest as "depredated" when nestlings or eggs were missing and the adults were still on the territory.

We mapped male territories using the minimum convex polygon (MCP, Mohr 1947, Odum and Kuenzler 1955, Barg et al. 2005). We defined the core of the territory as the area surrounding the nest-box the male advertised by singing. We defined its boundaries using song playback and observing male's movements inside its territory and by recording male's location during nest checks.

We considered a male to be polygynous if he was associated with more than one female whose incubation periods overlapped. To evaluate the importance of parental effort we recorded feeding rates when nestling were 2-3, 7-8, and 11-12 days old. We used Hi 8 video, camouflaged with grass and cloth to film parental activity. Cameras where placed 5-10 m from the nest approximately one hour after sunrise and the nest was filmed for four hours continuously. We later analyzed the videotapes and quantified the number of feeding trips to the nest for each nestling stage.

Comparisons of breeding parameters between populations

We used the synchrony index developed by Kempenaers (1993) to compare breeding synchrony between populations. This synchrony index (SI) can vary from 0%, when there is no overlap between breeding females, to 100%, when all the females in the population are breeding at the same time. When lay date was not observed directly, we calculated it based on length of the average incubation period (days between the laying of the last egg and the hatching of the last nestling) plus the clutch size (one egg is laid every day until clutch is completed). We calculated the number of fertile days for each female as the number of eggs laid. Females that bred twice during the same season were considered as two independent breeding females when calculating the SI. We calculated a mean female SI to compare synchrony between populations.

We compared clutch size, brood size, nestlings fledged, hatching success (brood size/clutch size), fledging success (nestlings fledged/nestling hatched), incubation period, and nestling period for monogamous nests of northern and southern house wrens. When comparing breeding variables, we excluded polygynous nests from the analysis because polygyny was rare in the southern house wren (see social

mating system). We calculated the incubation period as the number of days since the laying of the last egg to the hatching of the last nestling. We compared incubation periods only for nests that were checked every day during the hatching period and where all the eggs hatched. We calculated the nestling period as the number of days from the hatching of the first egg until the last nestling left the nest. Once house wren nestlings fledge they do not return to the nest. We only compared nestling periods for nests in which the first hatch and the last fledge date were known to the nearest day.

Paternity analysis:

We extracted genomic DNA from whole blood stored in lysis buffer using Perfect gDNA Blood Mini Kits (Eppendorf) or Qiagen DNeasy Blood and Tissue Kits (Qiagen) according to the manufacturer's instructions. We used polymerase chain reaction (PCR) to identify alleles at seven microsatellite loci: TA-A5-2, TA-A5-15, TA-B4-2, TA-C3(B)-2, and TA-C6-7 (house wren specific; Cabe and Marshall 2001), PCA3 (Dawson et al. 2000), and ThPl-14 (Brar et al. 2007). All loci were modified as in Makarewich et al. (2009) with the addition of a 5'-end fluorescent label (FAM, NED, PET, or VIC, Applied Biosystems) to the forward primer and the use of a "pigtailed" reverse primer. We PCR-amplified the first four loci together in a multiplexed panel and PCA3 and TA-C6-7 in a second panel; we amplified ThPl-14 individually. We carried out PCRs in 10 uL reactions consisting of 20 mM Tris, 50 mM KCl, 3.25 mM $MgCl_2$, 0.12 mM dNTPs, 0.025 U of Jumpstart Taq polymerase, and 0.3 pM each of the fluorescently labeled forward primer(s) and the corresponding pigtailed reverse primer(s). We used the following PCR protocol for all loci except ThPl-14: 1 cycle of 94°C for 3 min; then 35 cycles of 94°C for 1 min, 55°C for 1 min, and 72°C for 1 min; and finally 1 cycle of 72°C for 45 min. The protocol for ThPl-14

was identical except that the annealing temperature was increased from 55°C to 60°C. We analyzed labeled PCR products on a PRISM 3100 Genetic Analyzer (Applied Biosystems) and estimated allele sizes using a GeneScan-500 LIZ size standard. We viewed alleles on GeneMapper version 3.7 software (Applied Biosystems) and used Cervus version 3.0.3(Kalinowski et al. 2007) to determine the exclusion power of our microsatellite loci, whether they were in Hardy-Weinberg equilibrium, and the number of allele mismatches between each chick and its social father. We repeated the PCR amplification and genotyping analysis to confirm all social father mismatches; we considered extra-pair nestlings to be those with confirmed mismatches with their social father.

Statistical Analysis

We excluded from the present analysis all nests that during the study period were experimentally manipulated (males removed to test hypotheses regarding mating systems). We compared the proportion of polygynous males' breeding attempts and the proportion of nests with extra-pair fertilizations with Chi-squared tests. We tested for differences between populations in the proportion of extra-pair young per brood with a generalized linear mixed model (GLMM), specifying binomial distribution, logit link function and year as a random effect, weighted by the number of offspring per brood. We compared the mean female SI between populations with a Mann-Whitney U test and clutch size, incubation period, and nestling period with a mixed model, with year a fix effect and female as a random effect. We compared the proportion of successful nests and the proportion of nests that failed (because of predation, conspecific nest destruction, predation, or unknown causes) for northern and southern house wrens with a Chi-squared test. We looked for differences in

parental effort between populations by comparing the average number of adult feeding trips to the nest with Mann-Whitney U Tests. We carried out all statistical analysis in SPSS version 14.0 (SPSS 2005).

We estimated survival and recapture probabilities using Cormack-Jolly-Seber models (CJS) based on adult presence or absence in each year. We compiled capture histories for 427 adult birds (94 females and 139 males in the southern house wren and 109 females and 85 males in the northern house wren). We first built a general global model using the Program MARK that allowed survival (Φ) and recapture/ re-sighting (*p*) to vary with sex, year, and site. Then, we compared this model varying Φ and *p* (and combinations thereof) with models having a constant Φ and *p*. All models were constructed using the logit-link function (White and Burmanham 1999). We compared the models using Akaike's criterion (AICc) and we estimated the relative likelihood of each model with AIC weights (wi). We selected the model that presented the lower AICc and greater wi. We then assessed the goodness-of-fit (GOF) using a bootstrap (N = 500 simulations). This method allowed us to assess if the data fulfilled the assumptions of the model. From the simulations we estimated c-hat (c-hat = Variance of model/Variance of the mean of the simulations). This parameter controls for lack of fit to the model, caused by extrabinomial variation, since it reflects the overdispersion of data. We then used the derived QAIC (Akaike's information criterion adjusted for overdispersion) to make our final choice among competing models.

Results

Northern house wrens bred from the beginning of May (first eggs observed May 9th) until the end of July (last clutches observed in July 30th). Southern house bred from early October (first eggs observed October 9th) until mid- January (last eggs

observed January 15th). Hence, the southern house wren breeding season was 16 days (19%) longer. Northern house wrens bred slightly more synchronously than did southern house wrens (X_{SI}± SE = 12.02 ± 0.50, N = 225 and X_{SI} ± SE = 7.76 ± 0.32, N = 186, respectively, Mann-Whitney U test, Z=-5.52, $P < 0.001$).

Northern house wren social polygyny rate (% of male's breeding attempts that were polygynous) ranged from 13% to 40% across the study period (Table 1.1) while in the southern house wren, natural polygyny rate ranged from 0% to 2% (Table 1.2).

Table 1.1: Monogamous and polygynous male breeding attempts and polygyny rates for northern house wrens breeding in New York, US.

Year	Monogamous breeding attempts	Polygynous breeding attempts	Polygyny rate
2003	6	4	40%
2004	32	6	16%
2005	37	6	13%
2006	26	5	16%
2007	16	4	20%

Table 1.2: Monogamous and polygynous male breeding attempts and polygyny rate for southern house wrens breeding in Buenos Aires, Argentina.

Year	Monogamous breeding attempts	Polygynous breeding attempts	Polygyny rate
2003	56	1	2%
2004	42	1	2%
2005	30	0	0%
2006	33	0	0%
2007	38	0	0%

The social polygyny rate for northern house wrens was significantly higher than for southern house wrens (18%, N = 142 and 1% N = 201 respectively, $X^2 = 31.7$, $P < 0.001$). Similarly, the proportion of broods with extra-pair young was significantly

higher for the northern house wren than for the southern house wren (54%, N = 82 nests and 32%, N = 40 nests, respectively, $X^2 = 4.83$, $P = 0.028$) but did not differ significantly in the overall proportion of extra-pair young per brood (GLMM, $T_{(2)} = 1.62$, $P = 0.25$).

Southern house wrens made more trips to the nest per nestling than did northern house wrens. The mean feeding rate (feeding trips/hour/nestling) by southern house wrens was significantly higher during all three nestling periods measured (Table 1.3).

Table 1.3: Mean feeding rates per nestling at nests of northern (N-H) and southern (S-H) house wrens.

	Mean feeding rates (feedings/nestling hour) ± S.E.			
Nestling age (days)	N-H	S-H	Mann-Whitney U Test	
			Z	*P*
2-3	3.67 ± 0.18 (58)	4.44 ± 0.12 (48)	-4.669	< 0.001
7-8	5.23 ± 0.19 (43)	6.43 ± 0.21 (37)	-3.850	< 0.001
11-12	6.85 ± 0.32 (35)	8.00 ± 0.43 (33)	-2.019	0.044

The above difference holds because of brood size differences only (see below), as northern and southern house wrens did not differ in average number of feeding trips to the nest. The total mean feeding rate (feedings/hour) when nestlings were 2-3, and 7-8 days old did not differ significantly, despite a trend for northern house wrens to make more trips to the nest when nestling were 11-12 days old (Table 1.4 and Figure 1.1).

Northern house wrens had a mean clutch size of 6.03 ± 0.09 eggs (N = 119), and the incubation period averaged 13.94 ± 0.09 days (N = 34). The nestlings remained in the nest for an average of 15.89 ± 0.18 days (N= 53). Southern house wren clutch size was smaller, 4.81 ± 0.07 eggs (N = 114), but the incubation and

nestling periods were longer; 15.27 ± 0.15 days (N = 49) and 17.04 ± 0.22 days (N = 49), respectively. These differences were highly significant when controlling for adult and year effect (Table 1.4).

Table 1.4: Total mean feeding rates at nests of northern (N-H) and southern (S-H) house wrens.

Nestling age (days)	Mean feeding rates (feedings/hour) ± S.E. N-H	S-H	Mann-Whitney U Test *Z*	*P*
2-3	19.8 ± 1.06 (58)	18.2 ± 0.57 (48)	-1.00	0.317
7-8	27.7 ± 1.23 (43)	25.9 ± 1.12 (37)	-1.12	0.219
11-12	35.6 ± 1.86 (35)	30.7 ± 1.77 (33)	-2.02	0.059

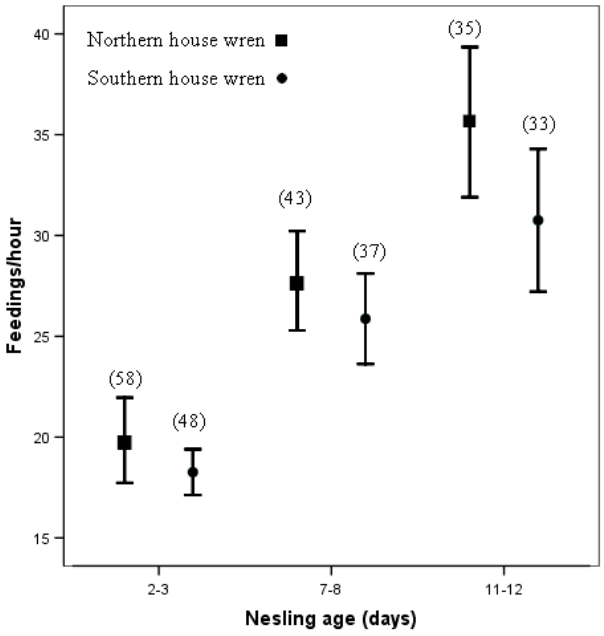

Figure 1.1: Mean ± SE feeding rate per nest of northern and southern house wrens at nests for 2-3, 7-8 and 11-12 days old nestlings. Sample sizes are given in parenthesis.

Southern house wrens were more likely to desert the nest or to fail because of predation or conspecific nest destruction than were northern house wrens (Table 1.6). As a result, nest success was significantly higher in northern house wrens (Table 1.6).

Table 1.5: Mixed model evaluating the differences in clutch size, incubation period and nestling period of northern (N-H) and southern (S-H) house wrens.

	N-H Least square means ± SE	S-H Least square means ± SE	General Mixed Model		
			DF	*F*	*P*
Clutch size	6.12 ± 0.09	4.92 ± 0.10	150	72.12	< 0.001
Incubation period	13.97 ± 0.19	15.20 ± 0.20	69	28.89	< 0.001
Nestling period	15.90 ± 0.19	16.92 ± 0.28	65	8.32	0.005

Table 1.6: Proportion of successful nests vs. unsuccessful nests that failed due to desertion, predation, conspecific nest destruction or unknown causes for northern (N-H) and southern (S-H) house wrens. Sample size is given in parenthesis.

	N-H (207)	S-H (150)	Chi-squared test	
			X^2	*P*
Desertion	4 % (9)	10 % (15)	4.43	0.035
Conspecific nest destruction	2% (4)	10 % (15)	11.23	< 0.001
Unknown causes of failure	1% (3)	9% (13)	10.58	0.001
Predation	5% (10)	15% (23)	11.43	< 0.001
Successful	87% (181)	56% (84)	44.94	< 0.001

Northern house wren territories were located at forest edges, woodlots, or areas with an abundance of bushes and had a maximum of two to three neighbors (Figure 1.2). Southern house wren territories were clumped in small forest patches surrounded by pastures, and most territories were in contact with several neighbors (Figure 1.3). Northern house wrens territories were dispersed over a larger area than were those of the southern house wrens (note the different scales in Figures 1.2 and 1.3).

Figure 1.2: Male northern house wren territories, Experimental Ponds Unit 1, Ithaca, NY, 2007.

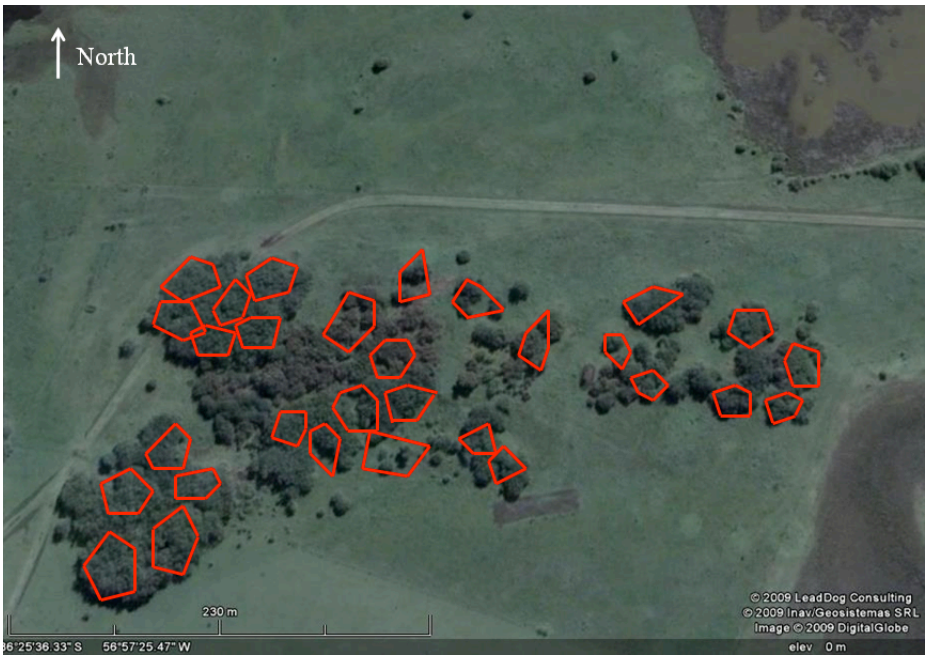

Figure 1.3: Males southern house wren territories, Buenos Aires, Argentina, 2004.

The estimation of average annual survival for southern house wren males was higher than for northern house wren males (X ±SE = 0.97 ± 0.025 vs. 0.48 ± 0.06). A similar pattern was observed between females; southern house wren females had higher adult survival than did northern house wren females (X ±SE = 0.91 ± 0.05 vs. 0.33 ± 0.07). We detected evidence of overdispersion (c-hat > 1) with our general global model, survival (Φ) and recapture/ re-sighting (p) varied with year, site, and sex (P=0.12*; observed deviance* = 35.59, *mean simulated deviance* = 27.03*; c-hat* = 1.31). Therefore we used QAIC*c* for model selection. Our best-supported model had wi of 0.75. In this model survival (Φ) differed by year, but not by sex or by site while recapture/ re-sighting (p) varied by year, sex, and sites. Hence, despite apparently large differences in survival estimates, our model does not support the hypothesis that significant difference exists in survival between north and south.

Discussion

Northern and southern temperate house wrens at our study sites differed in several life-history traits. Southern house wrens, like many tropical and southern temperate birds, were characterized by smaller clutches and longer incubation and nestling periods. Northern house wrens displayed life-history traits predicted for a northern temperate passerine, with bigger clutches and shorter incubation and nestling periods. House wrens also diverged in their social mating system, with social polygyny being rare in the southern house wren and fairly common in the northern form. Genetic polygamy was observed in both populations, however. Although a higher proportion of broods contained extra-pair young in the northern house wren, the proportion of extra-pair young per brood was not significantly different between the two sites. Southern house wrens made more trips to the nest with food per nestling,

suggesting a higher investment per nestling than northern house wrens, but other measurements (food quality and availability, nestling growth and development, and energy expenditure) were not examined, so this result must be interpreted with caution. In average number of trips to the nest, northern and southern house wrens did not significantly differ except near fledging, when northern house wrens made more trips to feed the young. This difference was probably a consequence of larger brood size in the northern house wren. Although we did observe a trend for southern house wrens to have higher adult survival, the difference was not statistically significant, presumably because of small sample sizes and large annual variation in re-sighting and recapture probabilities. Overlapping confidence intervals of each parameter and high standard errors caused the lack of fit to the model, and our estimation of survival parameters may not be accurate as the model has a low power.

Northern house wrens were more likely to fledge nestlings than were southern house wrens, since conspecific nest destruction, predation, and desertion all were less frequent in the north. Conclusions about relative predation rates in our populations must be drawn cautiously, as wrens in both areas were breeding in boxes that are relatively protected from predators, hence likely do not reflect the predation rates to which wrens have evolved when breeding in natural cavities. Higher conspecific nest destruction reflects greater competition for nesting sites, since house wren males usurp territories by pecking holes in eggs and killing nestlings (Freed 1986, Johnson and Kermott 1990).

Differences in northern and southern house wren mating systems are likely affected by differences in life-history traits. Social monogamy may be maintained in the southern house wren because male parental care is essential for defending the young from predators and infanticidal adults, or because male-male competition limits opportunities for males to monopolize more than one female, or both. In a population

where male-male competition is high, it may be difficult for a male to achieve breeding status by acquiring a territory, and even harder to acquire a territory and monopolize two females. These two aspects of male-male competition clearly are not mutually exclusive. Male competition in the south might be stronger than in the north, since southern house wren territories were clumped in small woodlots surrounded by grasslands (Figure 1.2) while northern house wrens were dispersed over a diverse habitat that included forest edges, patches of bushes, and dead forest fragments (all consequences of beaver activity; Figure 1.3). Although southern house wren males were clumped in small forest patches with more neighbors than northern house wrens, we did not observe higher rates of extra-pair fertilizations. This could be because southern house wren females do not engage more frequently in extra-pair copulations, or southern house wren allocate more time to mate-guarding, or both.

We suggest that migration may be a root cause of variation in house wren social mating systems. Northern house wrens are migratory and adults arrive at the study site only a few days before the onset of breeding. Males generally arrive before females and rapidly claim a territory and a nest-box, which they advertise by singing. Females arrive a few days later and settle in a territory to breed. The polygyny threshold model proposes that if female breeding success is determined by her mate's territory quality, then females often may breed with already mated males if compensated by the quality of the territory (Verner and Wilson 1966, Orians 1969). Moreover, females of migratory species might be constrained by time in choosing a mate, as they need to lay eggs rapidly if they are going to have a chance of producing two broods. In this situation, females might not have enough time to search for an unmated male or evaluate its mating status. In this case it may pay to breed in haste as a secondary female. Indeed, Johnson et al. (1994) found that, contrary to the key prediction of the polygynous threshold model, secondary females of northern house

wrens produced fewer offspring than females who chose nearby unmated males. This suggests that females may not be evaluating the prospects of compensation, and that they are simply time-constrained. By contrast, southern house wrens in Argentina are residents and remain in their territories year round. Females have considerable time to evaluate male mating status, update their knowledge of that status, and avoid already mated males. We suggest that higher density and non-migratory life history in southern house wrens causes greater male-male competition and provides enough time for females to evaluate male's social status before settling on a territory to breed. Future research should include manipulating male density in both migratory and resident populations in order to evaluate effects of male density on mating system.

Latitudinal variation in life-history traits within species has been reported previously within the northern hemisphere (e.g., tree swallows, *Tachycineta bicolor* (Dunn et al. 2000), great tits, *Parus major* (Sanz 1998) and flickers, *Colaptes auratus* (Koenig 1984)); between the northern hemisphere and the tropics (stonechats, *Saxicola torquata* (König and Gwinner 1995) and house wrens (Young 1994, Auer et al. 2007)) and between the subtropics and southern temperate (rufous-bellied thrushes, *Turdus rufiventris* (Ferretti et al. 2005)). This is the first paper to compare life history traits and mating systems within the same species in temperate zones of both hemispheres. In this case, southern and northern temperate populations differed in life-history traits in ways similar to differences between tropical and northern temperate species. Our study provides evidence that migratory life-history may play a fundamental role in this pattern.

We acknowledge that nest-boxes can affect several life-history traits, including clutch size, nest predation, adult survival, and polygyny rate (Møller 1989, Eadie et al. 1998, Purcell et al. 1997, Llambías and Fernández 2009). Still, data sets on birds breeding in nest-boxes provide access to good sample sizes and complete breeding

records on color-banded populations that are otherwise hard to obtain. Studies employing nest-boxes allow for comparisons between populations by reducing variation in certain variables (e.g. nest predation, entrance orientation, cavity size, and cavity quality), that are otherwise impossible to manipulate. Furthermore, the knowledge of how these traits are affected can help in designing experiments to test different hypotheses. Future comparisons of life history traits between northern and southern temperate birds, and their effects on mating systems, should be extended to include cavity nesters breeding in tree cavities, open cup nesters, and comparable non-migratory populations, to test our hypothesis about the role of male-male competition and migration in shaping social mating systems.

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CHAPTER 2

DO NEST-BOXES AFFECT SOUTHERN HOUSE WREN'S LIFE-HISTORY TRAITS?

Paulo E. Llambias and Gustavo J. Fernández

Abstract

Nest-boxes are known to increase clutch size, enhance breeding success and affect the social mating system of several cavity nesters. Although in recent years various cavity nesters have been studied in nest-boxes in South America, the effects of boxes on the study species' biology are unknown. To fill this gap we evaluated the effects of nest-boxes on the breeding biology and social mating system of southern house wrens (*Troglodytes aedon bonariae*) by comparing birds breeding in nest-boxes and tree cavities in two cattle ranches in Buenos Aires Province, Argentina. Southern house wrens nesting in boxes had higher breeding success but contrary to studies on the temperate zone we did not find differences in clutch size between wrens breeding in nest-boxes and tree cavities. The main causes of nest failure in tree cavities were nest predation and flooding of the cavity (70% and 23% of the failures respectively) while in nest-boxes predation and desertion were important causes of failure (38% and 34% of the failures respectively). The social mating system of southern house wrens is monogamy with biparental care, and neither was affected by the boxes. Males did not attract secondary females to additional nest-boxes; however, nest-boxes are safer breeding sites than tree cavities. These results suggest that nest quality alone might be not enough for secondary females to accept polygyny.

Introduction

Nest-boxes have provided researchers with large samples and detailed information on breeding biology and life history traits of cavity nesting birds. Indeed, several passerine species breeding in nest-boxes, including the pied flycatcher (*Ficedula hypoleuca*), blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*) in Europe and the tree swallow (*Tachycineta bicolor*), house wren (*Troglodytes aedon*) and eastern bluebird (*Sialia sialis*) in North America, have been intensively studied as model systems in life history evolution, population ecology and behavioral ecology. However the generality of these studies has been questioned based on the effects of nest-boxes on the species' biology and traits under study since nest-boxes can affect the social structure, reproductive competition and population dynamics of cavity nesters (Eadie et al. 1998). Nest-boxes have also played an important role in conservation since most cavity-nesting bird populations studied so far have shown an increase in population size when provided with nest-boxes (Purcell et al. 1997, Eadie et al. 1998).

Bird species breeding in nest-boxes often experience lower nest predation rates (Nilsson 1984a, b, Robertson and Rendell 1990, Møller 1989, Purcell et al. 1997), lay larger clutches (Nilsson 1984b, Robertson and Rendell 1990, Purcell et al. 1997, Fargallo et al. 2001) and fledge more nestlings (Nilsson 1986, East and Perrins 1988, Purcell et al. 1997, Fargallo et al. 2001) than birds breeding in tree cavities. By contrast, in some species like the ash-throated flycatcher (*Myarchus cinerascens*), nest-boxes seem to have no effect on breeding success (Purcell et al. 1997). Nest-boxes can also have a negative effect on breeding performance if boxes are easier to find by nest predators or brood parasites. In wood ducks (*Aix sponsa*) the frequency of intra-specific brood parasitism increased greatly in boxes erected in visible locations,

causing a reduction of hatching success when compared to boxes in visually occluded habitats (Semel et al. 1988, Eadie et al. 1998, Sherman 2001). However, in a highly territorial duck, the Barrow's goldeneye (*Bucephala islandica*), conspecific brood parasitism in visible boxes did not reach the same levels as in wood ducks, probably because it breeds at lower densities (Eadie et al. 1998). Nest-boxes might affect the rate of interspecific parasitism as well. In Colombia, house wrens breeding in boxes suffer from high frequencies of shiny cowbird (*Molothrus bonariensis*) parasitism when compared to tree cavities (Kattan 1997).

Since nest-boxes often are higher quality nesting sites than tree cavities, they can potentially affect the social mating system of cavity nesters and might offset the cost of social polygyny for secondary females (Johnson and Kermott 1991, Johnson et al. 1994). In species where males are constrained to social monogamy by the limitation of suitable nesting sites, the addition of nest-boxes might therefore increase the probability of social polygyny. For example, prothonotary warblers (*Protonotaria citrea*) are socially monogamous, but social polygyny can be induced by addition of nest-boxes to male's territories (Petit 1991). Similarly, in house wrens breeding in North America, nest-boxes increase the social polygyny rate when added to male's territories (Johnson and Kermott 1991). If males provided with extra breeding sites devote more time and energy to attracting secondary females, the presence of boxes might result in reductions in their parental care.

The purpose of this study was to determine how nest-boxes affect the breeding biology of the southern house wren (*Troglodytes aedon bonariae*). We investigated how boxes affected clutch size, breeding success, social mating system and parental roles by comparing pairs breeding in tree cavities with pairs that nested in nest-boxes in the same study areas in Argentina. Although in recent years there has been an increase in the use of nest-boxes for the study of southern temperate cavity nesters

(see Fraga 1992, Bulit and Massoni 2004, Moreno et al. 2005, Massoni et al. 2007, Moreno et al. 2007, Tuero et al. 2007), this study is the first to evaluate the effects of nest-boxes on the breeding biology of a southern temperate cavity nester.

Methods

Study species

The house wren is a small (12g), sexually monomorphic, territorial passerine that breeds in tree cavities, old holes excavated by other bird species, and man-made nest-boxes (Brewer 2001). Although formerly considered one species, with a breeding distribution ranging from Canada to Tierra del Fuego, it has been suggested that it should be split into three species: the northern house wren (*Troglodytes aedon*), the brown-throated house wren (*T. brunneicollis*), and the southern house wren, (*T. musculus;* Brumfield and Capparella 1996). In contrast to the northern house wren in which polygyny is common (Johnson 1998), the southern house wren is thought to be predominantly socially monogamous (Brewer 2001). However, all published descriptions of this birds' mating system have been based on tropical populations.

Study site

During October-January 2003-2006 we studied southern house wrens breeding in both tree cavities and nest-boxes in two cattle ranches (Los Zorzales and La Esperanza), 3 km apart, near the town of General Lavalle, Buenos Aires Province (36° 26'S, 56° 25'W), Argentina. We were unable to remain in the field during January but

we visited our field site several times to confirm that the breeding season did not extend into February.

In our study site, wrens occupy wooded areas surrounded by pastures, and the predominant tree species, *Celtis tala*, provides them with abundant tree cavities. We measured reproductive success and monitored social interactions in Los Zorzales during 2003-2004 and in La Esperanza during 2004-2006.

In Los Zorzales we studied wrens breeding in nest-boxes in a patch of three forest fragments (total area = 4.1 ha), each separated by ~50m of pasture. During early September 2003, we mapped all male territories (N = 47) in these plots, using song play-back to stimulate singing behaviour and observing each male's movements inside the territory to define the territory's core and agonistic interactions with neighbors to define its borders. Between September 12-15 2003 (30 days before the first egg was laid in the population), we erected 2 boxes on each male's territory (box density = 23 boxes/ha). To study wrens breeding in tree cavities we monitored a patch of four woodlots (total area = 4 ha), separated from each other by ~100m of pasture, located ~500m from the forest fragments to which nest-boxes were added.

In La Esperanza we studied a single 8 ha woodlot where we erected one box per territory ≈20 days previous to the appearance of the first egg in the population. During 2004 we installed 30 boxes (box density = 3.75 boxes/ha) and we added 63 boxes during 2005 resulting in total box density of11.65 boxes/ha. In the same plot we monitored wrens breeding in tree cavities on territories to which no boxes had been added.

Boxes were newly constructed from pine (roof, front and back) and *Eucalyptus* boards (laterals), with dimensions of 30.5 x 16.5 x 12.7 cm, with an entrance hole of 38 mm in diameter located in the front, just under the roof. When wrens accepted the boxes and started building nests we reduced the entrance hole diameter to 27 mm to

preclude the entry of shiny cowbirds since boxes are easier to locate by cowbirds than tree cavities and can suffer from high rates of multiple parasitism and egg destruction (Kattan 1997). We attached boxes with wire to main branches of trees, 1.7-2 m off the ground.

General Procedures

We searched for nests in tree cavities from early October until late December each year. We located nesting cavities using both behavioral cues from the adults and systematic searching. We checked nests in tree cavities every 2-4 days to assess clutch size, hatching success and fledging success. When nest contents could be observed directly, we considered a nest to have been preyed on if eggs or young disappeared well before fledging. We considered that a nest was deserted if both adults were observed alive and eggs were cold for more than two days or nestlings were dead inside the nest. We assumed that desertion was caused by flooding of the cavity if the nest was deserted after a storm and the cavity was flooded with dead eggs or nestlings inside. In tree cavities where nest contents could not be observed, we monitored the nest for at least 15 min on each visit and used adult activity to assess nest stage and fate. In our study site both shiny cowbirds and house wrens destroy eggs by pecking holes on them. When we observed whole clutches pecked inside nest-boxes we assumed they were destroyed by other wrens because the entrance hole was too small to admit cowbirds. When eggs were pecked inside tree cavities we assumed that it was caused by cowbirds if we observed cowbirds eggs and that it was caused by wrens if we observed the adults fighting with other wrens close to the nest or if we observed individuals that were not the territory holders inspecting the nest.

We checked nest-boxes every other day and recorded clutch size, number of nestling hatched, and number of nestling that fledged. When eggs were close to hatch and nestlings close to fledge we check the nests every day to calculate the incubation period (number of days since the laying of the last egg until the hatching of the first nestling) and the nestling period (number of days since the hatching of the first nestling until first nestling fledge).

We captured males with mist nets by stimulating aggressive behavior with song play-back. We captured females breeding in nest-boxes inside the boxes during incubation or feeding nestlings. We captured females breeding in tree cavities by setting a mist net close to the cavity entrance during the nesting stage. Since females were harder to capture with mist nets, fewer females were colored-banded in tree cavities than in nest-boxes (see below). We color-banded 86% of the males and 76% of the females breeding in boxes (225 breeding attempts), and 92% of the males and 40% of the females breeding in tree cavities (70 breeding attempts). We considered a male to be socially polygynous if two females nested on his territory and their incubation or nestling periods overlapped. We considered a male to be a bachelor if no females nested on his territory during the breeding season. To assess parental roles we monitored nests when nestlings were 2-3, 7-8 and 11-12 days old. On each visit we observed the nest until we saw both adults feeding. We used these short observations to confirm that both adults were attending the brood. In only two cases, the female was observed feeding alone, so we monitored the nest for 30 min to confirm that the male wasn't helping. Immediately after monitoring these nests, we located the males on the territory and followed them for 20 min to confirm that they were not feeding the nestlings.

House wrens usually produce a second clutch after a successful first clutch. We refer to them as first and second broods respectively. We could only assign nests to

first and second broods when both adults were color-banded early in the season and we were able to locate both nests.

Statistical Analysis

To test for differences in clutch size between nests built in tree cavities and nest-boxes we based our analyses mainly on nests found during laying (but see below) and excluded nests that were parasitized by shiny cowbirds, since cowbirds might reduce host clutch sizes when laying their eggs in the nest. To increase sample size of nests built in tree cavities we included 9 nests found during incubation as they did not show significant differences with those found during laying (Mann-Whitney test, $Z = -0.32$, $N_{laying} = 35$, $N_{incubation} = 9$, $P = 0.78$). To compare the number of nestlings hatched and fledged between tree cavities and nest-boxes we consider only nests that have produced at least one nestling or one fledgling. To increase sample size we included nests found during incubation. Since house wrens usually perform two nesting attempts in a breeding season, we checked for differences in clutch size, number of nestlings hatched and number of nestlings fledged between first and second broods with a paired analysis. To avoid pseudoreplication, when testing for differences in clutch size we only included the first brood for each breeding pair since we did not find significant differences between first and second broods (see Results).

We used a nested design to check for effects of year, plot, and nest type (nested within year and plot) on clutch and brood size, and fledgling number. We used a generalized linear model assuming a Poisson distribution of response variables (clutch size, brood size, and fledgling number), and a log link function. Year, plot and nest types were incorporated as nested predictor factors.

We estimated nest survival ($\hat{s}$) and daily mortality rates of nests built in tree cavities and boxes at different stages using Mayfield's methodology (Mayfield 1975) because we found some nests after the onset of incubation (see Results). When the nest was preyed upon between two consecutive visits, we estimated the time the nest survived as 40% of the length of the period between visits (Johnson 1979). We estimated the variance of $\hat{s}$ using Johnson's (1979) equation $V = [(DN - P).P]/DN^3$, where V is the variance, DN is the number of nest-days exposed and P is the number of nests that failed. We estimated the survival rate of the nest for three stages: egg laying (first-last egg laid), incubation (last egg laid-first egg hatched), and chick rearing (first egg hatched-first nestling fledged). We compared nest survival probability between early nesting attempts (initiation before November 15) and late nesting attempts (initiation November 15 to end of the field season). We compared the daily survival rates between different stages and between nests built in boxes and tree cavities using the program CONTRAST (Hines and Sauer 1989). The overall probability that one chick would fledge from nests built in boxes and tree cavities was estimated according to Mayfield (1975) as the sum of daily survival rates for each nesting stages elevated to the exposition time (number of days that the nest remain in that stage). We used an exposition time of 5 days for laying (mean laying period = 4.73, N = 239 nests), 14 days for incubation (mean incubation period = 13.62, N = 58 nests) and 16 days for nestling rearing stage (mean nestling stage = 15.88, N = 27).

Results

During 2003-2006 we found 70 nests in tree cavities: 35 during laying, 25 during incubation and 10 with nestlings. Of these 70 nests, we found 7 in La Esperanza and 63 in Los Zorzales (23 in plot Z1, 25 in plot Z2, 8 in plot Z3 and 7 in

plot Z4). We also monitored 225 nests in boxes, 170 since egg laying, 45 after the onset of incubation and 1 after the eggs hatched. Of these 225 nests, 118 were located in La Esperanza and 107 in Los Zorzales (12 in plot Z5, 20 in plot Z6 and 75 in plot Z7).

Based on nests that we found during the laying period so that we were able to estimate laying dates, our data suggest that most nesting attempts occurred early in the season and were initiated in boxes and tree cavities at about the same time. In Los Zorzales, average Julian lay date did not differ between nests built in boxes and tree cavities during 2003 ($N_{boxes} = 56$, $N_{cavities} = 10$, Mann Whitney U test, $Z = -0.04$, $P = 0.964$) and 2004 ($N_{boxes} = 43$, $N_{cavities} = 14$, Mann Whitney U test, $Z = -0.28$, $P = 0.781$).

Although boxes were newly constructed and installed 30 days before the laying of the first eggs in the population, there was no apparent delay in the use of boxes by House Wrens and box occupancy remained constant through the study period. Only 4 pairs bred in tree cavities when they were provided with nest-boxes in Los Zorzales (4.8% during 2003 and 5% during 2004; $X^2_1 = 0.003$, $P = 0.96$), and 7 pairs in La Esperanza (9.5% during 2004, 4.34% during 2005, and 6.25% during 2006; $X^2_2 = 0.69$, $P = 0.73$).

Of 70 nests in tree cavities, we determined the fate of 59. Of these 59 nests, 24 (40.7%) produced at least one fledgling. Among the 35 nests that failed we were able to determine the cause of failure of 30. The main causes of failure were predation (21 nests, 70%), desertion due to flooding of the cavity by rain (7 nests, 23%), and egg pecking by other house wrens (1 nest, 3%). One nest was deserted after we banded the female (it was excluded from the nest survival analysis). Of 43 nests in tree cavities that we could inspect, 7 (16.3 %) had cowbirds eggs.

We were able to determine the fate of 176 of the 225 nests built in boxes. Of these, 126 (72%) produced at least one fledgling. Of the 50 nests that failed we were able to determine the causes of failure of 47. The main causes of failure were predation (18 nests, 38%) and desertion for unknown reasons (16 nests, 34%). Other causes of failure were: human induced desertion (7 nests, 15%; these were excluded from the nest survival analysis) and egg destruction by other wrens (6 nests, 13%).

For wrens nesting in boxes there were no differences in nest survival for early and late nests or between nesting stages (Chi-squared tests, $P > 0.05$; Table 2.1). This pattern was independent of year (Chi-squared tests, $P > 0.05$ for all comparisons). Nest survival in tree cavities also did not vary between nesting stages or amongst early and late nests (Chi-squared tests, $P > 0.05$; Table 2.1).

Table 2.1: Mayfield estimates of daily nest survival rates (DSR) for southern house wrens breeding in nest-boxes and natural cavities. Nest survival probability indicates the probability of a nest to surviving the entire period of nesting (= DRS_{laying}^{5} x $DSR_{incubation}^{14}$ x $DSR_{nestling}^{16}$; see Mayfield 1975).

	Daily survival rate (± SE)				
Nesting stage	Laying	Incubation	Nestling	Overall nesting period	Nest survival probability
Nest-boxes	0.98 (0.006)	0.99 (0.002)	0.99 (0.002)	0.99 (0.001)	0.66
Natural cavities	0.94 (0.02)	0.97 (0.006)	0.96 (0.009)	0.97 (0.005)	0.25

Overall survival rates of nests built in boxes were higher than for nests built in tree cavities (Chi-squared tests, $\chi^2_1 = 18.41$, $P < 0.001$; Table 2.1). The overall probability that at least one chick would fledge from nests built in boxes was 0.66, whereas for nests built in tree cavities this probability was 0.25 (Table 2.1).

Clutch sizes of first broods in nest-boxes were similar to those of second broods (N = 35, mean = 4.67, SD = 0.69 and mean = 4.81, SD = 0.91, for first and second broods respectively, Wilcoxon paired test, Z = -0.6, *P* = 0.55). Number of nestlings hatched in the first brood and number of fledglings produced were also similar to those of second broods (N = 15, mean = 4.15 chicks, SD = 1.23, and, mean = 4.77 chicks, SD = 0.97, for first and second broods respectively, Wilcoxon paired test, *Z* = -0.63, *P* = 0.53; and N = 11, mean = 4.04 fledglings, SD = 1.22, and mean = 4.44 fledglings, SD = 1.15, Wilcoxon paired test, *Z* =-0.35, *P* = 0.73). We were unable to test differences in clutch, brood size and number of fledglings produced between first and second broods in natural cavities due to a low sample size for second broods (N = 9 for clutch size; N = 4 for brood size; and N = 2 for number of fledglings).

Nest built in boxes had an average of 4.85 ± 0.79 eggs (mean ± SD; N = 148) and hatched 4.58 ± 1.01 chicks (mean ± SD; N = 140), whereas nest built in tree cavities had 4.45 ± 0.85 eggs (mean ± SD; N = 35) and hatched 3.83 ± 0.41 chicks (mean ± SD; N = 8). Mean number of fledgling produced in boxes was 4.26 ± 1.06 (mean ± SD; N = 127) whereas those produced in tree cavities was 3.88 ± 0.64 fledglings (mean ± SD; N = 8). We did not find any effect of year, plot or nest type (nest-box or tree cavity) on the clutch size, brood size or number of fledgling produced (Table 2.2).

Based on nesting survival and pooled mean number of fledglings produced per nesting attempt, pairs breeding in boxes produced on average 2.93 young per attempt whereas the average for pairs breeding in tree cavities was 1.08 nestlings per attempt.

During 2003-2004 the number of territories held by males (N = 47) in Los Zorzales did not change after we provided them with two boxes per territory. In 2003 the 47 male territories were defended by 42 mated males and by 5 bachelor males, and

in 2004 the 47 male territories were defended by 40 mated males and 7 bachelor males.

Table 2.2: Generalized linear models evaluating the effects of year, plot (La Esperanza or Los Zorzales), and nest type (nest-box or tree cavity; nested within year and plot) on the clutch size (number of eggs laid), brood size (number of nestlings hatched in nests that produced at least one nestling) and number of fledglings (number of nestling fledged in nests that produced at least one fledgling) for house wren nests built in boxes or tree cavities. All models assumed a Poisson error structure in the response variable (logit link function).

Factor	*d.f.*	X^2	*P*
Clutch size			
Year	3	1.08	0.78
Plot	1	0.48	0.49
Nest type	5	0.8	0.98
Brood size			
Year	3	0.23	0.97
Plot	1	0.43	0.51
Nest type	5	2.69	0.75
Fledgling number			
Year	3	1.89	0.59
Plot	1	3.20	0.07
Nest type	5	2.09	0.83

In Los Zorzales during 2003, the proportion of bachelor males (36%) was significantly higher in plots that contained only tree cavities than in plots provided with nest-boxes (11.9%, Chi-square test, $\chi^2_1 = 6.70$, $P = 0.01$). Likewise in 2004, the proportion of bachelor males (45.16%) was significantly higher in natural-cavity plots than in nest-box plots (14.89%; Chi-square test, $\chi^2_1 = 8.70$, $P = 0.003$).

In tree cavities the social mating system of the 70 monitored nests was social monogamy. We never observed a male associated with more than one female or advertising a cavity to attract a secondary female. Among nest-box plots, we observed three instances of social polygyny in 216 breeding attempts (1%) where we were able

to determine the social mating system. In two of these cases, the males took over a territory of a neighboring female after the disappearance her mate. In the third case we were unable to determine how the male became polygynous. We never observed males advertising for the second nest-box on their territories, nor any females attempting to breed in them.

We monitored parental behavior at 37 tree cavities with nestlings 2-3 days old, 21 with nestlings 7-8 days old, and 18 with nestlings 11-12 days old. We observed both adults feeding at 36 of these 37 nests (97%). In the one exceptional case, the male never fed nestlings and he was observed singing from different parts of his territory although he did not seem to be advertising any particular cavity. We monitored parental behavior at 48 nest-boxes with nestlings 2-3 days old, 33 boxes with nestlings 7-8 days old and 36 boxes with nestlings 11-12 days old. We observed both adults feeding at 47 of these 48 nests (98%). As in tree cavities, no male was observed to advertise for a second cavity.

Discussion

Similarly to studies of cavity nesters in the northern temperate zone (see Purcell et al. 1997), our study in the southern temperate revealed that house wrens nesting in boxes had a higher breeding success than in tree cavities. As reported by Auer et al. (2007) for a southern house wren population breeding in tree cavities in northern Argentina, the primary cause of nest failure in tree cavities was predation. Additionally, in our study site, flooding was also an important cause of failure since most tree cavities were branch scars located on the main trunks of *Celtis tala* trees, and, during heavy rain, water running down the tree trunks inundated the cavities and caused mortality of eggs and nestlings and desertion by parents.

New nest-boxes seem to be immediately accepted as breeding cavities by southern house wrens in our study site. Between 1-3 days after we erected nest-boxes we observed males defending them. Indeed, 95.2% of the house wrens bred in boxes during the first year of study. This fact might be related to low quality of tree cavities in our study site.

Northern house wrens breeding in boxes in North America lay larger clutches and have lower predation rates than those nesting in tree cavities (Purcell et al. 1997, Johnson and Kermott 1994). When boxes were attached to trees in Wyoming, nesting success did not differ significantly from tree cavities, but nesting success was higher in boxes mounted on greased (predator-deterrent) metal poles (Johnson and Kermott 1994). In our study site, although nest-boxes were located on trees, the probability of nest survival was significantly higher than in tree cavities. Differences in nest survival between Wyoming and Buenos Aires for nest-boxes attached to trees might be due to differences in the predator communities and dimensions of the entrance. Although we reduced the diameter of the entrance hole primarily to avoid cowbird parasitism, it also apparently excluded some predators. The overall breeding success of southern house wrens in tree cavities in our study site was low (25%) when compared to reports from other populations of both northern house wrens (63% in Wyoming, Johnson and Kermott 1994, and 70% in Arizona, Li and Martin 1991) and southern house wrens (65% in northern Argentina, Auer et al. 2007). Low breeding success in our site might be due to differences in the predator community, size and location of cavities and weather patterns. The fact that southern house wrens and other cavity nesters studied so far have higher breeding success when breeding in nest-boxes is not surprising since nest-boxes reduce losses to predation and inundation during storms.

Contrary to other studies of cavity nesters (see Nilsson 1984b, Robertson and Rendell 1990, Purcell et al. 1997, Fargallo et al. 2001), we did not find differences in

clutch size between nests built in boxes and those built in tree cavities. The facultative adjustment in clutch size observed in these other studies might be attributed to a cavity area effect, since the bottom area of nest-boxes is often larger than in tree cavities and several bird species have shown an increase in clutch size with nest bottom area (Slagsvold 1982, van Balen 1984). Still, other studies did not find such a relationship (Alatalo et al. 1988, Purcell et al. 1997). Since we did not measure the bottom area of nests we cannot discard that the lack of differences could be caused by similar nest's areas between tree cavities and nest-boxes.

The social mating system of the southern house wren was previously studied by Freed (1986a,b, 1987) in nest-boxes in Panama. Freed (1986b) reported that during his 4-year study, 95% of birds paired socially monogamously and 5% were socially polygynous. Although all territories in his study site had two or more nest-boxes, none of the polygyny cases he recorded involved females settling on the territory of an already mated male. Rather, social polygyny occurred when a male seized the territory and mate of a neighbor. We observed a similar pattern in our southern temperate site. Although we did not observe socially polygyny in tree cavities, three cases of social polygyny occurred in nest-boxes. At least two of them involved a male adding the territory and female of a neighboring male.

Like Freed (1986a,b, 1987), we provided some males with extra nest-boxes, but none of these males attracted a secondary female. This contrasts with the behavior of the northern house wren in which mated males become socially polygynous by advertising and attracting females to multiple nesting sites in their territories, both in populations breeding in tree cavities and nest-boxes (Johnson 1998, Johnson and Kermott 1991). We also found that in the southern house wren, the proportion of bachelor males was lower in plots provided with nest-boxes than in plots where wrens were breeding in tree cavities. This may indicate that females preferred territories with

nest-boxes or the males that defended box-containing territories, or (probably) both. Although pairs remained in the same territories year round, we observed at least three instances of females leaving a male in the tree cavity plots and pairing with a male with a nest-box on his territory. Conversely, we have never observed a female deserting a male with a nest-box to breed in a tree cavity. In the northern house wren there is experimental evidence that females partially base their mate choice on nest-site characteristics (Johnson and Searcy 1993, Eckerle and Thompson 2006). It has been suggested that secondary northern house wren females choose already mated males with nest-boxes because the quality of nest-boxes might compensate for the cost of polygyny, (Johnson and Kermott 1991). It is surprising though, that, given that nest-boxes are better breeding sites than tree cavities and that females seem to prefer males with nest-boxes, social polygyny is so rare in the southern house wren even when nest-boxes are provided. This pattern might be caused by the superabundance of nest-boxes since most females will be able to find a male with a nest-box in its territory and breed as a primary female. Future research should explore this possibility by creating high quality territories with nest-boxes surrounded by territories with tree cavities.

In summary, our study suggests that nest-boxes in the southern temperate zone might have different effects on the breeding biology of cavity nesters as boxes in the northern hemisphere. In our study population, nest-boxes were not associated with larger clutch sizes but wrens breeding in boxes did have higher breeding success. Although nest-boxes did not affect the social mating system, it did affect female choice since males provided with boxes were more attractive to females than males defending territories with tree cavities. In view of the fact that nests in tree cavities have lower fledging success, birds breeding in boxes probably spend more energy in feeding young but they get a greater payoff in reproductive success for doing so.

Future research should focus on the effects of nest-boxes on adult survival and energy expenditure as well as the ecological and behavioral variables that are constraining southern house wrens males to social monogamy. Social monogamy does not necessary implies genetic monogamy and many socially monogamous species have broods containing extra-pair young (review in Griffith et al. 2002). Several paternity studies have been done on birds breeding in nest-boxes (see Weeton et al. 1987, Morton et al. 1990, Kempenaers et al. 1992, Dunn and Robertson 1993, Lifjeld et al. 1993) although the frequency of extra-pair paternity can be overestimated. Indeed, boxes might be at higher densities than tree cavities, distributed more uniformly and attract a greater percentage of experienced females (Barber et al. 1996). On the other hand, Barber et al. (1996) study in tree swallows did not find an effect of nest-boxes on extra-pair paternity rate. The authors assessed the frequency of extra-pair paternity as the percentage of broods with at least one extra-pair young in 25 families breeding in tree cavities in Ontario, Canada. When compared to a nearby population breeding in nest-boxes, broods in tree cavities with extra-pair paternity contained a significantly greater proportion of extra-pair young but the frequency of nests with extra-pair paternity did not differ between both populations. Although house wrens have been intensively studied, the effects of nest-boxes on the genetic mating system still remain to be tested in both the northern and southern temperate zones

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CHAPTER 3

NORTHERN AND SOUTHERN HOSUE WRENS ARE FACULTATIVELY MONOGAMOUS

Paulo E Llambias

Abstract

I studied the social mating system and parental behavior of a polygynous population of northern house wrens (*Troglodytes aedon aedon*) in the U.S. and a monogamous population of southern house wrens (*Troglodytes aedon bonariae*) in Argentina. To evaluate the role of biparental care in maintaining social monogamy I induced polygyny in the southern house wren by removing males from their territories. If the need for biparental care is constraining the mating system, monogamy should be obligate (male care essential) in the southern house wren and facultative (male care dispensable) in the northern house wren. In both populations, females feeding nestlings alone were able to increase feeding rates and fully compensate for the lack of male aid during one third of the nestling stage. Northern house wren females without male help during the first half of the nestling stage and secondary females produced as many fledglings as aided females and monogamous females respectively. Southern house wren females without male help fledged as many nestlings as aided females from nests that produced at least one nestling, but significantly fewer when considering all nesting attempts. However, secondary southern house wren females produced as many fledglings as did monogamous females. Polygynous males in both populations fledged significantly more nestlings than did monogamous males. Thus,

monogamy is facultative in both populations, and other ecological factors might be constraining southern house wrens males to monogamy.

Introduction

Differences in mating systems are often associated with differences in parental care (Davies 1993, Cézilly and Danchin 2008). Approximately 90% of bird species are socially monogamous (Lack 1968, Gill 2007), but extra-pair fertilizations are widespread and the social mating system differs from the genetic mating system (Sherman 1981, Wesneat and Sherman 1990, Westneat and Stewart 2003). In social monogamy, a male and a female form a pair bond and provide care to the young. In social polygyny, a male mates with more than one female and secondary females often receive less help from males in raising their brood (Clutton-Brock 1991, Johnson et al. 1993, Pribil and Searcy 2001). The apparent cooperation between socially monogamous pairs in raising a brood is remarkable since natural selection should often favor individuals that increase their fitness by seeking additional mating opportunities (Maynard Smith 1977, Houston et al. 2005, Olson et al. 2008). Indeed, social monogamy is a rare mating system and is only common in birds (Mock and Fujioka 1990). Several hypotheses have been proposed to explain how monogamy can be maintained despite selection for polygyny. In obligately monogamous species, biparental care is essential for breeding success; however, in facultatively monogamous species, females can raise at least some young with limited or no male assistance (Kleiman 1977, Runcie 2000). When biparental care is not essential, males might still be monogamous if female fertility is synchronous within the population so that secondary females are not available after males have mated with their primary female (Emlen and Oring 1977). Males' territories may also be of similar quality so

that it will be better for a female to pair with an unmated male (Wittenberger and Tilson 1980). Alternatively, monogamy can be maintained by female choice, if unpaired females avoid settling with paired males (Whittenberger and Tilson 1980, Dale and Slagsvold 1994) or if resident females prevent additional females from settling in the territory (Whittenberger 1981, Sandel and Smith 1997, Cézilly et al 2000).

Research programs aimed at understanding why a particular bird species is socially monogamous must first identify the type of monogamy under study, because if it is obligate, testing multiple hypotheses concerning the advantages of polygyny would be inappropriate. However, characterization of monogamy has been more difficult than expected. The classic approach has been to remove males during different stages of the nesting period to quantify the effects of loss male care on growth and survival of chicks (see review Bart and Tornes 1989). But a male-removal experiment does not necessarily mimic polygyny. First, polygyny does not always mean total desertion of one of the broods, as secondary females may receive some male help in raising the brood (Nolan 1978, Temrin and Jakobsson 1988, Leonard 1990, Johnson et al. 1993). Second, males might not feed the brood of a secondary female but still defend the nest against predators or conspecifics. In the northern house wren (*Troglodytes aedon*), females who settle with already-mated males receive similar aid in defending the nest as do females who settle with unmated males (Johnson and Albrecht 1993). For these reasons, a better way to evaluate whether monogamy is facultative or obligate is to induce polygyny in an otherwise monogamous population and analyze its costs and benefits to males and females separately (see Smith et al. 1982, Greenlaw and Post 1985, Veiga 1992).

The objective of this study is to begin to explore the evolution of social monogamy in southern house wrens by evaluating whether male care is essential for

reproduction by inducing polygyny in an otherwise monogamous population. I then compared the costs and benefits of polygyny for each sex with a northern house wren population where polygyny is frequent. The house wren is an excellent species for studying the relationship between parental care and mating systems. Whether it is considered as a single species or as a complex of closely related species (see *study species* below), geographic variation in social behavior will be largely the result of differences in environmental factors rather than phylogenetic differences in species' biology. Northern house wrens occur from Canada to northern Mexico, are migratory, and a substantial number of males are polygynous (Johnson 1998), whereas the southern house wren, with a distribution from Central America to Tierra del Fuego, is mainly sedentary, and polygyny is very rare (Freed 1987, Llambías and Fernández 2009).

If monogamy is obligate in the southern house wren and facultative in the polygynous northern house wren then the following predictions should be met: (1) artificially induced secondary southern house wren females will be unable to fledge any nestlings; and (2) polygynous southern house wren males will have similar or reduced success compared to monogamous males, whereas polygynous northern house wren males will have greater breeding success than monogamous ones.

Methods

Study species

House wrens are small (11-13g), sexually monomorphic, insectivorous, territorial passerines. They breed in tree cavities, holes excavated by other bird species, and man-made nest-boxes (Brewer 2001). Although the house wren was

formerly considered one species, with a breeding distribution ranging from Canada to Tierra del Fuego, it has been suggested (Brumfield and Capparella 1996) that the species should be split into three species: the northern house wren (*Troglodytes aedon*), the brown-throated house wren (*T. brunneicollis*), and the southern house wren, (*T. musculus*).

At my study sites (2003-2007), males were provided with multiple boxes, and polygyny rate per male breeding attempt in the southern house wren was 1% (2/201), compared to 18% (27/142) in the northern house wren. In the northern house wren, polygyny occurs most commonly when monogamous males advertise from a secondary nest that they built on their territory, thus attracting a secondary female (Johnson 1998). In the southern house wren, the rare instances of polygyny occur when a male takes over the territory and mate of a neighbor, either by evicting or replacing its owner. Cases of second females settling on a territory of an already mated male have never been observed (Freed 1986, Llambías and Fernández 2009) nor have I seen males advertizing for secondary mates at surplus nest sites. Although take-over and replacement by challenging males has been described in the northern house wren (Johnson and Ketmott 1990), this is not a common means for males to become polygynous in these populations.

Study sites

I carried out research on the northern house wren breeding in wooden nest-boxes near Ithaca, New York State, US (42° 28'N, 76° 29'W), and on the southern house wren near General Lavalle, Buenos Aires province, Argentina (36° 26'S, 56° 25'W).

During May-August 2003-2008 I studied northern house wrens on mixed deciduous patches of forests at Cornell experimental ponds Units 1 and 2, separated by 3 km. Previous to the breeding season, I erected nest-boxes on greased poles, 1.5m high, and 25-50m apart (2-3 boxes per male territory, 68 boxes erected at Unit 1 in 2003 and 60 at Unit 2 in 2004).

I studied southern house wrens in Buenos Aires province on coastal woodlands at a private cattle ranch, "Los Zorzales", during October-January 2003-2007. The study site was described by Llambías and Fernández (2009). I worked in three forest fragments (total area = 4.1 ha), each separated by ~50m of pasture. During early September 2003 and prior to the erection of nest-boxes, I mapped all male southern house wren territories (N = 47) in these plots. I used song play-back to stimulate singing behaviour and I observed each male's movements inside the territory to define the territory's core, and agonistic interactions with neighbors to define its borders. During September 12-15, 2003 (~30 days before the first egg was laid in the population), I erected 2 boxes on each male's territory.

Field procedures

At both my North and South American sites, I trapped adult wrens inside nest-boxes or with mist nets set on the territory. Each year I color-banded 77-80% of the breeding adults for individual identification. I checked nest-boxes every other day and recorded relative lay date (day one was considered as the first egg laid in the given year), clutch size, brood size, and number of nestlings fledged. I classified a nest as preyed upon when nestlings or eggs were missing and nest material was disturbed, and I classified nests as a takeover (conspecific nest destruction) when eggs had small holes pecked in them or dead nestlings were found close to or inside the nest-box with

marks of pecking on the head. I classified a nest as deserted if nestlings were found dead inside the nest and both adults were recorded alive, and successful if at least one nestling fledged from the nest. I defined the potential breeding success for each monogamous male as the total number of nestlings produced from its mate's nest and the potential breeding success of polygynous males as the total number of fledglings produced by each male's primary and secondary females. Unfortunately, I do not have measures of extra-pair fertilizations rates for polygynous nests of southern house wrens that were created by adult removal, since to avoid further disturbance I did not take blood samples from those nestlings and adults.

I considered a male to be polygynous if he was associated with more than one breeding female whose incubation or nestling periods overlapped. The first female to lay eggs was defined as the primary female. Primary females are generally assisted by the male in raising the brood whereas secondary females receive reduced or no assistance (Johnson and Kermott 1993). Since polygyny is rare in Buenos Aires, I induced it experimentally by removing males from the population during 2004, 2005 and 2007. Before egg-laying (6-8 days before the first egg was recorded), I captured with mist nets a total of 26 males from 26 monogamous territories and translocated them 50km away. Males were kept in individual cardboard boxes (19x15x12cm) and released within two hours of capture. Six males returned to their territories, but I excluded these nests from further analyses of parental care. If a non-territorial male (floater) occupied an open territory, I removed this male as well. Male removal experiments and procedures were approved by the Institutional Animal Care and Use Committee (protocol number: 20576-EM), Cornell University. No males were harmed during tranlocations. As a consequence of male removals, 10 females bred as secondary females of 10 neighboring monogamous males, who expanded their territories to incorporate their widowed neighbor and became polygynous. Note that

females were not necessarily forced into polygyny, since each year between 4-7 territorial males were unpaired and defending territories within the 4.1ha forest patch where the removals were done.

I used Hi 8 video-cameras to record parental behavior. I filmed nest-boxes continuously for four hours, when nestlings were 2-3, 7-8 and 11-12 days old, using camouflaged cameras placed 5-10 m from the nests one hour after sunrise. Later analysis of videotapes enabled me to identify the color-banded adults and quantify the number of male and female feeding trips. I defined a feeding trip as an adult entering the nest-box with food in its bill and emerging without the food, and a brooding bout as a female remaining inside the nest-box for more than 60 seconds. I calculated the average length of each female's brooding bout for each session (four hours video) and the average number of brooding bouts at nests with and without help when nestling were 2-3 days old. I left out of the analysis four northern house wren and three southern house wren nests where adults did not resume feeding during the first 15 minutes of recording, because this indicated that the placement of the camera was disturbing the birds. Six videos in which it was not possible to identify the adults by color bands also were not analyzed.

To determine the effects of male parental care on female breeding success, I compared several reproductive variables (see below) of nests with or without male help, independent of their mating status. For this analysis, I consider a nest as without male help if the male was not observed feeding the nestlings at all during the first half (0-8days) of the nestling stage. During the first half of the nestling stage, male parental care is critical since nestlings cannot fully thermoregulate and females are unable to increase feeding rates and brood the nestlings at the same time (Johnson and Kermott 1993). I also analyzed the effects of mating status by comparing the same reproductive

variables between monogamous females (mated with monogamous males) and secondary females (second females mated to polygynous males).

Statistical methods

I compared the feeding rates (feedings/nestling/hour) of females with or without male help across chick ages using Mann-Whitney U Tests. I compared brooding time and number of brooding bouts of females with or without male help using a general linear model (GLM) with number of nestlings as a fixed factor. To test for differences in breeding variables (lay date, clutch size, brood size and number of nestlings fledged) between nests with or without male help and between monogamous and secondary females I used a GLM, with year, help or no help and mating system as fixed factors respectively. I analyzed whether monogamous and secondary females differed in the proportion of nests with or without male help with a Chi-squared test. I also used a Chi-squared test to compared the proportion of successful nests and the proportion of nests failed (because of nest predation, conspecific nest destruction, predation or unknown causes) for secondary and monogamous females and for females with and without male help. I used Yates' correction when the data violated the assumptions of the Chi-squared test.

I used a Mann Whitney *U* test to test for differences between populations in the average number of days between the laying of the first eggs of the primary and secondary females. I compared numbers of fledglings produced by polygynous and monogamous males with a GLM using year and social status as fixed factors. All statistical analyses were carried out in SPSS version 14.0 (SPSS 2005).

Results

Southern house wren females without male help fed nestlings at significantly higher rates (female feedings/nestling/hour) than did females with male help when nestlings were 2-3, 7-8 and 11-12 days old (Fig. 3.1).

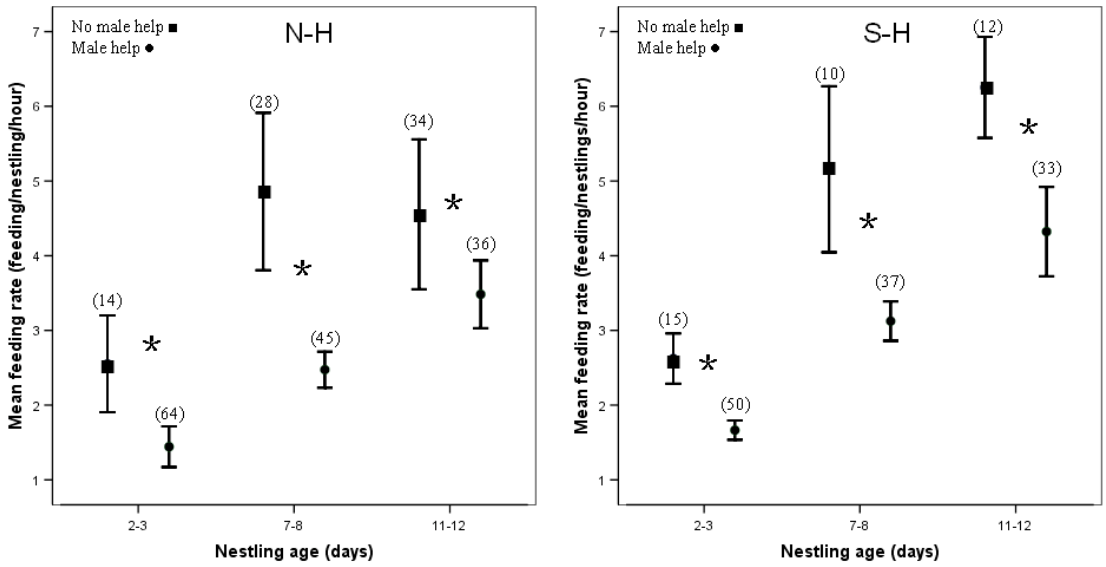

Figure 3.1: Mean ± SE feeding rates of females northern (N-H) and southern (S-H) house wren at nests with or without male help for 2-3, 7-8 and 11-12 days old nestlings. Asterisks (*) represent groups that are significantly different ($P < 0.005$) following Mann-Whitney *U* Test. Sample sizes are given in parenthesis.

The higher feeding rates of unaided females did not fully compensate for the lack of male help when nestlings were 2-3 and 11-12 days old, and the total feeding rates (total feedings/nestling/hour) during these stages were significantly lower at nests without male help (Fig. 2). However, there were no significant differences in total feeding rates between nests with or without male help when nestlings were 7-8 days old (Fig. 3.2).

Northern house wren females without male help spent significantly less time brooding than did females with male help ($X \pm$ SE = 350.25 ± 41.62 s $N = 14$ and $X \pm$

SE = 489.47 ± 22.79 s $N = 63$ respectively; GLM, $F_{75} = 103$ $P = 0.009$), but they did not differ significantly in the number of brooding bouts ($X \pm$ SE = 20.36 ± 1.72 $N = 14$ and $X \pm$ SE = 18.38 ± 0.58, $N = 63$ respectively; GLM, $F_{75} = 1.82$, $P = 0.180$). Southern house wren females without male help also spent significantly less time brooding than did aided females ($X \pm$ SE = 366.06 ± 26.69 s, $N = 15$ and $X \pm$ SE = 456.91 ± 18.67s, $N = 50$, GLM; $F_{63} = 5.98$, $P = 0.017$), and they made significantly more brooding bouts ($X \pm$ SE = 24.20 ± 1.08, $N = 15$ vs. $X \pm$ SE = 19.78 ± 0.55, $N = 50$; GLM; $F_{63} = 14.22$, P □0.001).

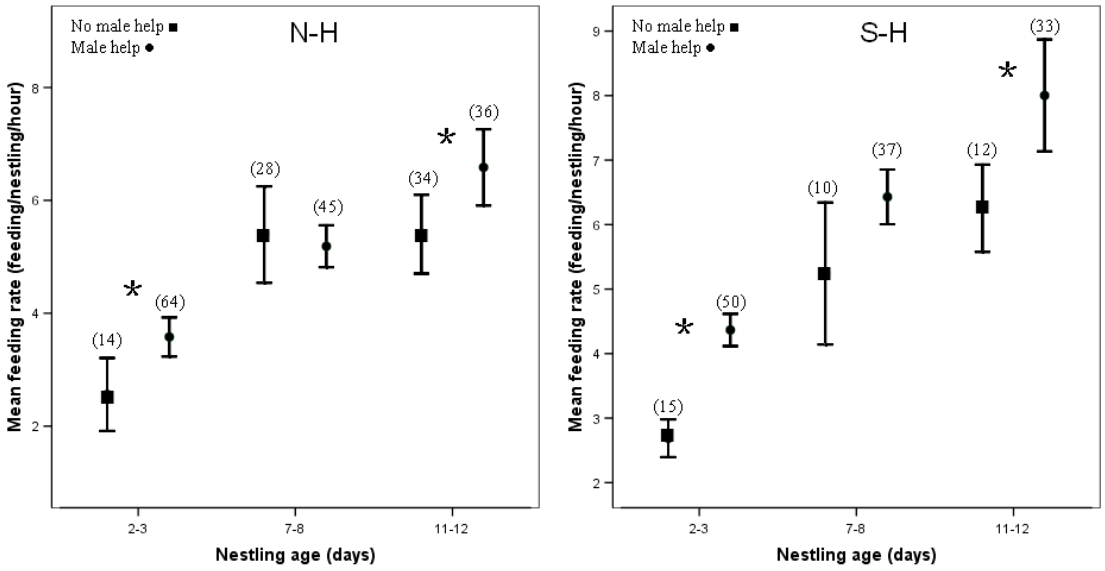

Figure 3.2: Mean ± SE feeding rates of females northern (N-H) and southern (S-H) house wren at nests with or without male help for 2-3, 7-8 and 11-12 days old nestlings. Asterisks (*) represent groups that are significantly different ($P < 0.05$) following Mann-Whitney U Test. Sample sizes are given in parenthesis

Females who did not receive male help for the first half of the nestling stage were either monogamous or secondary females (12 secondary and two monogamous in the northern house wren and seven secondary and nine monogamous in the southern house wren). There were no significant differences in the frequencies of secondary females who did not received male help between northern and southern house wrens

(86%, $N = 14$ vs. 100 %, $N = 7$, respectively; Yates' $X^2 = 0.07$, $P = 0.793$). Differences in the frequencies of monogamous females who did not receive male help also were not significant (7%, $N = 30$ and 20%, $N = 44$, respectively; Yates' $X^2 = 1.70$, $P = 0.192$). In the northern house wrens, females that did not receive male help for the first half of the nestling stage all produced at least one fledgling and they did not significantly differed in lay date, brood size or number of fledglings produced (Table 3.1).

Table 3.1: Breeding variables of northern house (N-H) and southern (S-H) wren nests with or without male help.

		Without male help Mean ± SE (N)	With male help Mean ± SE (N)	General Linear Model	*P*
N-H	Relative lay date	30.62 ± 6.55 (13)	31.61 ± 3.79 (28)	$F_{36} = 0.21$	0.649
	Clutch size	6.14 ± 0.23 (14)	6.00 ± 0.14 (37)	$F_{46} = 0.13$	0.723
	Brood size	5.64 ± 0.31 (14)	5.56 ± 0.18 (37)	$F_{46} = 0.02$	0.901
	Fledge number	4.83 ± 0.37 (14)	5.30 ± 0.20 (37)	$F_{46} = 1.65$	0.206
S-H	Relative lay date	21.71 ± 3.93 (14)	21.62 ± 2.01 (37)	$F_{46} = 0.02$	0.899
	Clutch size	4.56 ± 0.24 (16)	4.78 ± 0.08 (40)	$F_{51} = 0.38$	0.542
	Brood size	4.00 ± 0.32 (15)	4.38 ± 0.13 (40)	$F_{50} = 2.02$	0.161
	Fledge number (all nests)	2.13 ± 0.50 (16)	3.75 ± 0.19 (40)	$F_{51} = 4.15$	0.047
	Fledge number (successful nests)	3.40 ± 0.43 (10)	3.95 ± 0.14 (38)	$F_{43} = 0.88$	0.353

In southern house wren, females without male help were more likely to fail due to conspecific nest destruction and were less likely to produce at least one fledgling (Table 3.2), yet these females did not differ from aided females in lay date, brood size or number of fledglings produced from successful nests (Table 3.1). However, when considering all nests, the trend for nests that received early male help to fledge more nestlings was not significant (Table 3.1).

Table 3.2: Proportion of successful and unsuccessful nests that failed due to desertion, predation, conspecific nest destruction or unknown causes, for females with or without males help of southern house wrens.

	No help ($N = 16$)	Help ($N = 40$))	Chi-squared test	
			X^2	P
Desertion	0.06	0.05	0.22	0.639
Predation	0.00	0.00		
Conspecific nest destruction	0.19	0.00	4.66	0.039
Unknown failure	0.06	0.00	0.22	0.639
Successful	0.69	0.95	5.00	0.025

Secondary northern and southern house wren females did not differ significantly from monogamous females in lay date, clutch size, brood size, or number of fledglings produced, whether viewed over all nest attempts or only successful nests (Table 3.3, note that the sample of successful secondary nests is too small in southern house wrens to draw any conclusions).

In northern house wrens, secondary females were more likely to desert the nest or fail due to conspecific nest destruction, but there were no significant differences in the proportion of nests that fledged at least one young or failed due to predation or unknown causes of failure (Table 3.4). In southern house wrens, the proportion of successful nests and nests that failed due to desertion, predation, conspecific nest

destruction and unknown causes did not differ significantly between secondary and monogamous females (Table 3.4).

Conspecific nest destruction was more frequent in non-manipulated nests of southern than northern house wren (10% of 150 nests vs. 2% of 207 nests respectively; $X^2 = 11.23$, $P < 0.001$).

Table 3.3: Breeding variables of monogamous and secondary northern (N-H) and southern (S-H) house wren females.

		Secondary females Mean ± SE (N)	Monogamous females Mean ± SE (N)	General linear model	P
N-H	Relative lay date	29.52 ± 3.48 (23)	26.59 ± 1.84 (125)	$F_{142} = 0.18$	0.670
	Clutch size	6.20 ± 0.19 (25)	5.96 ± 0.09 (140)	$F_{159} = 0.52$	0.470
	Brood size	5.50 ± 0.35 (22)	5.40 ± 0.12 (126)	$F_{142} = 0.01$	0.943
	Fledge number (all nests)	4.79 ± 0.44 (24)	4.53 ± 0.17 (135)	$F_{153} = 0.01$	0.957
	Fledge number (successful nests)	5.48 ± 0.26 (21)	5.05 ± 0.12 (121)	$F_{136} = 0.47$	0.492
S-H	Relative lay date	28.56 ± 3.33 (9)	31.33 ± 1.80 (147)	$F_{151} = 0.69$	0.408
	Clutch size	5.00 ± 0.17 (9)	4.84 ± 0.06 (183)	$F_{186} = 2.19$	0.141
	Brood size	4.43 ± 0.30 (7)	4.38 ± 0.12 (103)	$F_{104} = 0.10$	0.748
	Fledge number (all nests)	2.50 ± 0.719 (10)	2.32 ± 0.18 (143)	$F_{148} = 0.13$	0.717
	Fledge number (successful nests)	4.00 ± 0.45 (5)	4.05 ± 0.12 (82)	$F_{81} = 0.03$	0.856

Northern and southern house wrens did not differ significantly in the average number of days between the laying of the first egg of primary and secondary females ($X \pm$ SE = 12 days ± 1.40, N = 22 and $X \pm$ SE = 15.30 days ± 3.79 N = 10, respectively; Mann Whitney U test, Z= -0.27, P = 0.785).

Table 3.4: Proportion of successful and unsuccessful nests that failed due to desertion, predation, conspecific nest destruction or unknown causes, for monogamous and secondary females of northern (N-H) and southern (S-H) house wrens.

		Secondary females (N = 25)	Monogamous females (N = 143)	Chi-squared test X^2	P
N-H	Desertion	0.04	0.03	4.33	0.037
	Predation	0.04	0.05	2.67	0.102
	Conspecific nest destruction	0.04	0.01	9.27	0.002
	Unknown failure	0.00	0.01	0.16	0.685
	Successful	0.88	0.89	0.05	0.823
S-H	Desertion	0.20	0.10	0.21	0.6428
	Predation	0.00	0.15	0.76	0.3827
	Conspecific nest destruction	0.20	0.10	0.21	0.6428
	Unknown failure	0.00	0.09	0.14	0.7082
	Successful	0.60	0.56	0.01	0.9330

When considering the success of primary and secondary females together, northern house wren polygynous males fledged significantly more nestlings than did monogamous males ($X \pm$ SE = 9.74 ± 0.75, N = 23 vs. $X \pm$ SE = 4.53 ± 0.17 N = 135, respectively; GLM, F_{152} = 90.73, P □ 0.001; Fig. 3). Similarly, southern house wren polygynous males fledged significantly more nestlings than did monogamous ones (X ± SE = 4.90± 0.78, N = 10 and $X \pm$ SE = 2.32 ± 0.18; N = 143 respectively, GLM, F

$_{147} = 14.34$, $P < 0.001$; Figure 3). All polygynous southern house wren males lost their secondary females to bachelor' males in the following breeding event.

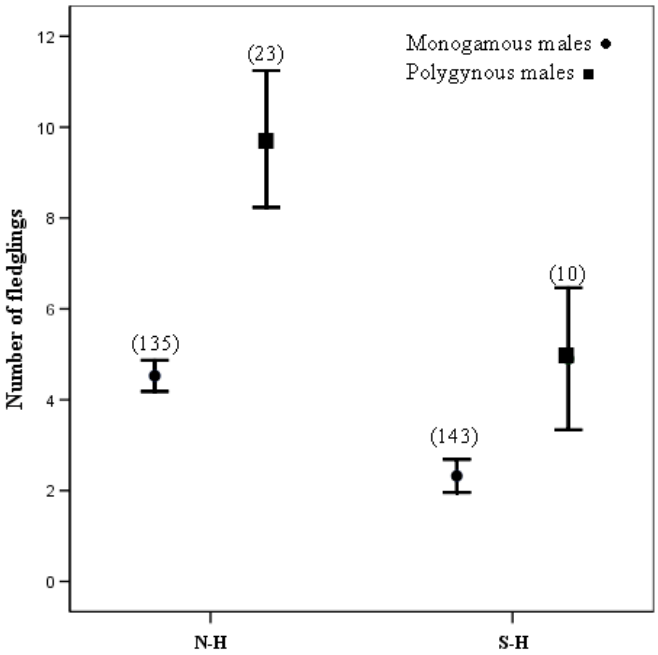

Figure 3.3: Number of fledgling produced by polygynous and monogamous males of northern (N-H) and southern (S-H) house wren. Sample size are given in parenthesis

Discussion

Monogamy in the southern house wren is facultative, since the two predictions of obligate monogamy were falsified. (1) Artificially induced secondary southern house wren females fledged as many nestling as did monogamous females and (2) polygynous males in both southern and northern wrens fledged more nestlings than did monogamous males. I was unable to measure rates of extra-pair fertilizations in these polygynous nests, and reproductive success of polygynous and monogamous males might not differ significantly if polygynous males are unable to guard their females effectively from extra-pair copulation attempts (Arak 1984). However, in the

northern house wren, polygynous males are more successful than monogamous males when the lost of paternity is taken into consideration. Soukup and Thompson (1997) reported that northern house wren polygynous males sire more nestlings in the two nests they attend than do monogamous males when considering their success by combining primary and secondary nests. Poirier et al. (2004) studied a different population of northern house wrens and concluded that although polygynous males are more likely to be cuckolded, they still sired more young than did single-brooded monogamous males. At my study sites the proportion of control broods with extra-pair young was significantly greater for northern than for southern house wrens, hence the loss of paternity for polygynous southern house wren males might be similar or even smaller than in northern house wrens (chapter 1). Future research should try to measure the loss of paternity among southern house wren polygynous-induced males.

Both in the polygynous northern house wren and in the monogamous southern house wren, non-aided females were able to increase feeding rates during the nestling period and compensate for the lack of male help in feeding the young when nestlings were 7-8 days old (Fig. 3.1 and 3.2). If primary and secondary females nests do not completely overlap in time, as is usually the case in house wrens, males might be able to provide parental care during the most critical stages of the nestling period (2-3 and 11-12 days old). Other components of parental care might be important in maintaining monogamy, since male presence can be essential in nest defense against predators. Wrens at my study sites were breeding in nest-boxes protected from predators, hence is impossible to determine if nest predation is more prevalent in southern house wrens. If nest predation is high and males are effective in deterring nest predators, they might be unable to defend more than one nest effectively. Polygynous males and secondary females might have lower breeding success than monogamous individuals as a result. I did not observe this in my present study, and experimental evidence suggests that

secondary females in the northern house wren don't receive less help than do females mated to monogamous males in defending the nest from model snakes (Johnson and Albrecht 1993). But future research in the south should determine whether male parental care is essential in defending offspring from predators.

Male house wrens usurp territories by evicting the resident male and removing eggs and killing the nestlings. (Freed 1986, Johnson and Kermott 1990). Male nest defense might thus have major implications for the maintenance of monogamy in the species. The nest defense hypothesis proposes that secondary females obtain less help from mates in defending offspring from conspecifics (Johnson and Kermott 1993), so higher rates of nest destruction in secondary females or females without male help can be expected. Indeed, southern house wren females without male help and secondary northern house wren females were more likely to fail due to conspecific nest destruction. Thus, male presence might be important in nest defense in both populations. When considering breeding success of unmanipulated nests, conspecific nest destruction was more frequent in the southern than in the northern house wren, suggesting more competition for nesting sites in the south.

Male parental care in the house wren is important in both populations because it reduces the losses of eggs and nestlings to infanticidal adults, still females in both populations were able to raise at least some young without male help and polygynous males seems to fledge more young than do monogamous ones. Although I did not find significant differences in the number of fledglings produced by secondary and monogamous females, lower feeding rates at non aided female's nests might have compromised both adult and juvenile survival and/or investment in future reproduction. In Panama, where wren polygyny is very rare, Freed (1986) also reported that, fledging success of secondary females did not differ from that of monogamous females and that polygynous and monogamous males also did not differ

in success, although there was a trend toward polygynous males and monogamous females being more successful. In sum, data from both southern temperate and tropical house wrens indicate that biparental care is not essential for producing at least some young, hence monogamy is probably maintained by other factors.

Previous research indicates that the cost of male desertion varies between sites or between seasons at the same site in the northern house wren. In a two-year study, Bart and Tornes (1989) removed males when nestlings were 4-5 days old and found that nestling survival was reduced only in hard weather conditions when food abundance was low. In Wyoming, Johnson et al. (1992), removed males much earlier, during the second half of the incubation stage, and reported that widowed females produced 32% fewer fledglings per egg laid than did control females. In a later study in the same population, without male removals, Johnson and Kermott (1993) showed that poorly aided females decreased brooding time and increased feeding rate, yet the mean feeding rate at poorly aided nests was significantly lower than at fully aided nests. Both the present study on northern and southern house wrens and Johnson and Kermott (1993) show that poorly aided or non aided females reduce brooding time, probably to increase feeding rates, but this increment is not enough to compensate for the lack of male help. Additionally, the present study showed that non-aided northern and southern house wren females are also unable to compensate for the lack of male help when nestlings were close to fledging. This lack of compensation toward the end of the nestling period is not caused by brooding requirements since brooding is uncommon after nestlings are 7 days old. Rather, it seems that non-aided females reach the maximum feeding rate by day 7 and are unable or unwilling to increase feeding rates later in the nestling stage (Figures 1and 2).

Not surprisingly, the cost of polygyny also varies between populations of northern house wrens. Secondary females in Wyoming produced significantly fewer

fledglings than did monogamous and primary females (Johnson et al. 1993). However, Quinn and Holryd (1992) and this study did not find significant differences in the number of nestlings fledged between secondary and monogamous females. There might still be a hidden cost of polygyny in terms of juvenile or adult survival, and these costs are likely to vary across the northern house wren range. Male removal experiments and natural cases of polygyny in two populations of tree swallows (*Tachycineta bicolor*) suggest that food abundance affects the cost of polygyny; females without male help produce fewer offspring where food is less abundant (Dunn and Robertson 1992).

In sum, the polygyny rate of the house wren complex varies geographically, being higher in the North America to lower in Central and South America. This variation in social mating system seems not to be caused by the need for biparental care since studies from several populations have shown that biparental care is not essential and that it is shareable. Other ecological variables, including distribution of females and resources in space and time, male-male competition or female-female aggression, might be responsible for maintaining monogamy in the southern house wren. Conspecific nest destruction is more frequent in the southern house wren, and male removal experiments there induced polygyny. However all the experimentally polygynous males eventually lost one of their females to intruding males, suggesting that male-male competition might play a crucial role in southern house wren mating systems.

Studies of house wrens have provided researchers with several insights into the interactions between parental care and mating systems. The needs for biparental care are dynamic, not only might they change between years and across geographic ranges but also across an individual breeding attempt. Biparental care might be essential when nestlings are too young to thermoregulate or later when their food requirements

are high. The uneven distribution of the needs of biparental care across the nestling stage makes male care sharable, since a male with two females that do not overlap completely in their nesting phenology can switch among nests in feeding nestlings of the highest need. Attempts to evaluate the importance of biparental care in monogamous mating systems should try to analyze its benefits and costs at different nesting stages. Other components of parental care (like nest defense from predators and infanticidal adults) should be taken into consideration in future research as they might be important in maintaining monogamy.

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CHAPTER 4

FACULTATIVE MONOGAMY IN THE SOUTHERN HOUSE WREN IS MAINTAINED BY INTRASEXUAL COMPETITION

Paulo E. Llambias

Abstract

The preponderance of social monogamy in birds is remarkable since males should often be selected to increase their fitness by reducing parental care and becoming polygynous. It has been suggested that monogamy can be maintained in a population if: 1) biparental care is essential for breeding success, 2) female fertility is synchronous within the population, 3) resources are evenly distributed so that male's territories are of similar quality, 4) male-male competition prevents males from acquiring more than one female or 5) female-female aggression prevents additional females from settling in monogamous territories. To explain why social polygyny is widespread in the northern house wren but rare in the southern house wren, I studied and compared populations breeding in the U.S. and Argentina. Previous research had shown that biparental care is not essential in house wrens, thus monogamy is not obligate. The results of both experiments and geographical comparisons between these populations suggest that the social monogamy of southern house wrens is maintained by two processes: male-male competition and female-female aggression. Female synchrony could not explain the prevalence of polygyny in the northern house wren since the northern birds were significantly more synchronous than southern house wrens. The addition of nest-boxes to increase territory quality did not induce polygyny in southern house wrens, although breeding success was higher in nest-

boxes and wrens preferred them to tree cavities. Male removal experiments increased the polygyny rate in the southern house and suggested that the preponderance of floater males was greater in the southern than in the northern house wren, indicating intense competition for breeding territories. Finally, northern and southern house wrens visited a caged female close the primary and secondary box in similar proportions and both were aggressive to the female close to the primary nest-box, but a higher proportion of southern house wren females were aggressive when the cage was placed close to the secondary box. Southern house wren polygynous males' territories were of similar size to northern house wren territories, but monogamous southern house wren territories were smaller than northern house wren territories, suggesting that southern house wren males need to monopolize large territories to be polygynous. In summary, social polygyny is rare in the southern house wren because competition between males does not allow the monopolization of bigger territories and multiple females, and female-female aggression prevents males with smaller territories from acquiring more than one female.

Introduction

Differences in mating systems are generally associated with differences in parental care (Davies 1993, Cézilly and Danchin 2008). In social monogamy, a male and a female form a pair bond and both take care of the young. In social polygyny, a male mates with more than one female and secondary females often receive less help from males in raising the brood (Clutton-Brock 1991, Ligon 1999, Johnson et al. 1993, Pribil and Searcy 2001). Approximately 90% of bird species are socially monogamous with biparental care (Lack 1968, Gill 2007), but the assumption that social monogamy reflects the genetic mating system has been overturned by the discovery of the widespread occurrence of extra-pair fertilizations in otherwise monogamous birds (Sherman 1981, Westneat and Sherman

1990, Westneat and Stewart 2003). The preponderance of social monogamy in birds and the apparent cooperation between mates in raising a brood is remarkable, since natural selection should often favor males that increase their fitness by reducing parental care and becoming polygynous (Maynard Smith 1977, Mock and Fujioka 1990, Houston et al. 2005, Olson et al. 2008).

Social monogamy can be obligate if biparental care is essential for breeding success or facultative if females can raise at least some young without care from the male (Kleiman 1977, Runcie 2000). Several hypotheses have been proposed to explain how monogamy can be maintained even when male parental care is not essential. The female breeding synchrony hypothesis (Emlen and Oring 1977) states that if female fertility is synchronous within the population, males will be unable to monopolize multiple females because, after courtship and mating have occurred with the primary female, potential secondary females will have already been inseminated. Monogamy can also be maintained by resource distribution (Emlen and Oring 1977, Davies 1993). If female breeding success is determined by her mate's territory quality, females will breed with an already mated male if they are compensated by obtaining better territories than they could with any available unmated males (Verner and Wilson 1966, Orians 1969). Thus, to explain monogamy, the male territory quality hypothesis proposes that when male territories are of similar quality, males will be unable to monopolize more than one female since it will always be better for a female seeking a mate to pair with an unmated male (Wittenberger and Tilson 1980). Alternatively, monogamy can be the outcome of male-male competition. If habitat is saturated by males, competition for mates can be strong enough to prevent males from monopolizing more than one female at a time (Freed 1987). Finally, female aggressive behavior can maintain monogamy if any additional female attracted to a male's territory is inhibited from settling by the aggression of the resident female (Wittenberger and Tilson 1980, Cézilly et al. 2000, Cézilly and Danchin 2008).

Previously, I have shown that monogamy is facultative in two house wren (*Troglodytes aedon*) populations that differ in polygyny rate: the southern house wren with a natural polygyny rate of 0-1% and northern house wren with a polygyny rate of 16-40% (chapter 3). When polygyny was induced in the southern house wren, females were able to fledge nestlings with reduced male help and polygynous males were more successful than monogamous males. The same pattern was observed in the northern house wren, when natural cases of polygyny were analyzed. Thus biparental care is not essential for breeding success and monogamy is facultative in both populations. Here I tested if female synchrony, territory quality, male-male competition and female-female aggression can explain differences in polygyny rate between populations. Under the female breeding synchrony hypothesis (Emlen and Oring 1977) females in polygynous populations should breed less synchronously than those in monogamous populations, and in the present case, female southern house wrens would breed more synchronously than northern house wren females. The male territory quality hypothesis (Wittenberger and Tilson 1980) predicts that monogamy results from insufficient variation in territory quality, and if monogamy is a consequence of homogeneity in territory quality, increasing the quality of target territories in the south should induce polygyny and decreasing the quality of territories of polygynous northern house wrens should result in monogamy. The male-male competition hypothesis predicts that competition between males for achieving breeding status should be stronger in the southern house wren than in the northern house wren and that removing males from the southern house wren population should induce polygyny. This hypothesis also predicts that the percentage of floater males (males unable to acquire a territory to breed) in the population should be higher in the southern than in the northern house wren. Finally, the female-female aggression hypothesis predicts that southern house wren females will be more aggressive to each other than northern house wren females, thus preventing additional females from settling in their territories.

Methods

Study species

House wrens are small (11-13g), sexually monomorphic passerines that breed in natural tree cavities, cavities excavated by other bird species, and man-made nest-boxes (Brewer 2001). Its widespread distribution, from Canada to Southern Argentina, has led to suggestions that the species should be split into three distinct species: the northern house wren (*Troglodytes aedon*), the brown-throated house wren (*T. brunneicollis*) and the southern house wren (*T. musculus*) (Brumfield and Capparella 1996).

The northern house wren, which is migratory, occurs from Canada to northern Mexico, and 15-35% of the males breed polygynously (Johnson 1998). The southern house wren, which is mainly sedentary, occurs from Central America to Tierra del Fuego and 1-15% of males breed polygynously (Freed 1986).

Study sites

I studied house wrens that bred in nest-boxes on coastal woodlands near General Lavalle, Buenos Aires province, Argentina (36^{o}26'S, 56^{o} 25'W) and in mixed deciduous patches of forest near Ithaca, New York, US (42^{o} 28'N, 76^{o} 29'W).

During October-January 2004-2007 I studied southern house wrens at a private cattle ranch, "Los Zorzales." I worked in eight forest fragments separated by 50-150m. During early September 2003, I mapped all male territories (N = 47) in three of the fragments (nest-box plots), using both observations of male-male aggressive interactions and responses to song playback to define each territory's core and borders. Then I erected two boxes on each male's territory, 30 days before the first egg was laid in the population.

I attached boxes to trees at heights of 1.5-2.8m. I studied wrens breeding in natural cavities in the five remaining fragments. However, to increase territory quality, in 2004 I added two boxes to half the territories that were occupied by pairs (N = 24; see territory quality manipulation below). All boxes were attached with wire to main branches of trees, 1.7-2m off the ground. After wrens had started building a nest inside the nest-box I reduced the entrance hole diameter from 38 to 27 mm to preclude parasitism by shiny cowbirds (*Molothrus bonariensis*).

During May-August, 2003-2008, I studied northern house wrens in New York State, at Cornell University's Experimental Ponds Units 1 and 2, separated by 3 km. Before wrens arrived in spring, I erected nest-boxes on greased poles, 1.5m high and 25-50m apart (68 boxes erected at Unit 1 in 2003 and 60 at Unit 2 in 2004). Since northern house wrens are migratory, it was not possible to map territories before the breeding season. For this reason, some male northern house wrens ended up monopolizing 2-3 boxes per year.

Field procedures

Each year in both populations I color-banded 77-90% of the breeding adults for identification. I trapped adults inside the nest-boxes and with mist nets set on the territory. Every other day I checked boxes and recorded lay date, number of eggs laid (clutch size), number of nestlings hatched (brood size) and number of nestlings fledged (fledging number).

I considered a male to be polygynous if I observed more than one female nesting on his territory and their incubation or nestling periods overlapped. I did not analyze cases of serial polygyny where a male bred with two different females in sequence but their incubation, nestling, or fledgling periods did not overlap. I considered a female to be

primary or secondary based on lay dates (primary females started their breeding attempt earlier than did secondary females).

Territory area measurements

I measured the areas of male territories at both sites (2004, 2005 and 2007 in Argentina and 2006-2007 in the US). I mapped male territories using the minimum 95% convex polygon (MCP) method by excluding 5% of the locations furthest from the nest to avoid spurious excursions (Mohr 1947, Odum and Kuenzler 1955, Barg et al. 2005). To calculate the territory area I connected the outermost locations using the track function on a GPS (Garmin Vista HCx). I used song playback to map male territories. I observed male's movements during two sessions of 15 minutes after stimulating aggressive behavior for five minutes. To complete the polygon, I recorded the location of the male during each nest check. All birds were followed between dawn and 1230 hrs EDT.

Male removal experiments

To evaluate the prevalence of floaters in both populations I removed mated territorial males and compared the proportion of floaters that settled in these territories after removal. I assumed that unbanded males were floaters since I captured and color banded between 85-90% of all territorial males prior to the removal experiments. None of the few pre-existing unbanded territorial males abandoned or expanded their territories after male-removals on nearby territories. All the males I removed were associated with a female in early stages of nest building. Between 24-48 hrs after removal, I identified the new owner of the territory by observing singing behavior or interactions with neighbors. In a few cases I stimulated singing behavior with song playback. Here I report data only for

territories that were occupied within 48 hrs by a new male with a female who remained on the same territory when the owner was replaced. If the female deserted the territory or no male was recorded within 48 hrs after male removal, I excluded these females and territories from the analysis.

In 2007 and 2008 in New York, I collected 17 territorial males (carcasses were deposited at the Cornell University Museum of Vertebrates). Nine males were removed at the beginning of May (early season) and eight in June-July (late season). In Argentina in 2004, 2005, and 2007, I captured 31 males in October (early season) and 13 males in November-December (late season) and released them 50 km away in the botanical gardens of San Clemente del Tuyu. Five translocated males that subsequently returned to their territories were excluded from the analysis.

Female-female aggression experiments.

During 2006-2007 in Buenos Aires and 2007-2008 in New York I evaluated the importance of female-female aggression using a simulated intruder. I captured females in early incubation to use them as intruders for two sessions of 20 minutes each and then released them back on their territories. All females used in these experiments survived and within 2 days had either started a new nest or resumed incubation.

To conduct the experiments, I installed a cage (20x15x15cm, with a water container) containing an "intruding female" close to the primary nest-box (box where the resident female was breeding) or close to secondary nest-box (box inside the territory, 25-40 m away from the primary box, where a secondary female would likely breed if she were able to settle in the territory). The cage was hung from a tree branch, 1.8-2m from the ground, 5m from the nest-box, and its cover was removed at the beginning of the intrusion trial. I observed the cage from a distance of at least 50m with 10x42 binoculars and

recorded if the cage was attacked (resident female hit the cage with legs or wings) or approached (resident female perched no farther than 5m from the cage). All resident females tested for aggression were in early incubation (3-7 days from the laying of the last egg). I kept the simulated intruding female in a cage covered with a dark cloth when transporting it between territories.

Territory quality manipulation.

During 2004 in Argentina, I experimentally increased the quality of a fraction of monogamous territories to create heterogeneity in territory quality. In five wood patches (total area = 5 ha) where pairs were breeding in natural cavities I added two nest-boxes to 12 territories. Each patch was separated by at least 100 m of pasture from each other and together contained 34 male territories, 24 occupied by pairs and 10 defended by bachelor males. I installed the boxes inside the territory as far as possible from each other yet less than 7m from the territory edge.

Synchrony index

I used the synchrony index (SI) developed by Kempenaers (1993) to compare breeding synchrony between populations. The SI can vary between 0%, when there is no overlap between breeding females, to 100%, when all the females in the population are breeding at the same time. When lay date was not directly observed, I calculated it based on length of the average incubation period (days between the laying of the last egg and the hatching of the last nestling) plus the clutch size (one egg is laid every day until clutch is completed). I consider the number of fertile days for each female as the number of eggs

laid. Females that bred twice during the same season were considered as two independent breeding females when calculating the synchrony index.

Statistical Analysis

I compared the mean female synchrony index between populations with a Mann-Whitney U test. I compared the proportions of floaters and attacking and approaching females using Chi-squared tests. I compared male territory sizes between populations with a general linear model (GLM) using site and year as fixed factors. I performed all statistical tests with SPSS version 14.00 (SPSS 2005).

Results

Northern house wrens bred more synchronously than did southern house wrens (SI ± SE = 12.02 ± 0.50, N = 225 vs. 7.76 ± 0.32, N = 186, respectively, Mann-Whitney U test, Z=-5.52, $P \square 0.001$; Figure 4.1). The population SI for northern house wrens ranged from 12.37 % to 17.8%, whereas southern house wren breeding synchrony ranged from 9.02% to 9.18%.

In every case after a male removal, the territory was occupied by a floater or by a territorial male. Territorial males were either males that expanded their territory (62% in the northern house wren, N = 13 and 69% in the southern house wren, N = 13) or moved in after abandoning their former territory (38% in the northern house wren, N = 13 and 31% in the southern house wren, N = 13).

The removal experiments suggested that floaters were more abundant in the southern house wren population than in the northern house wren. During both early and

late breeding season, the proportion of territories occupied by floaters after male removal was significantly higher in southern house wrens.

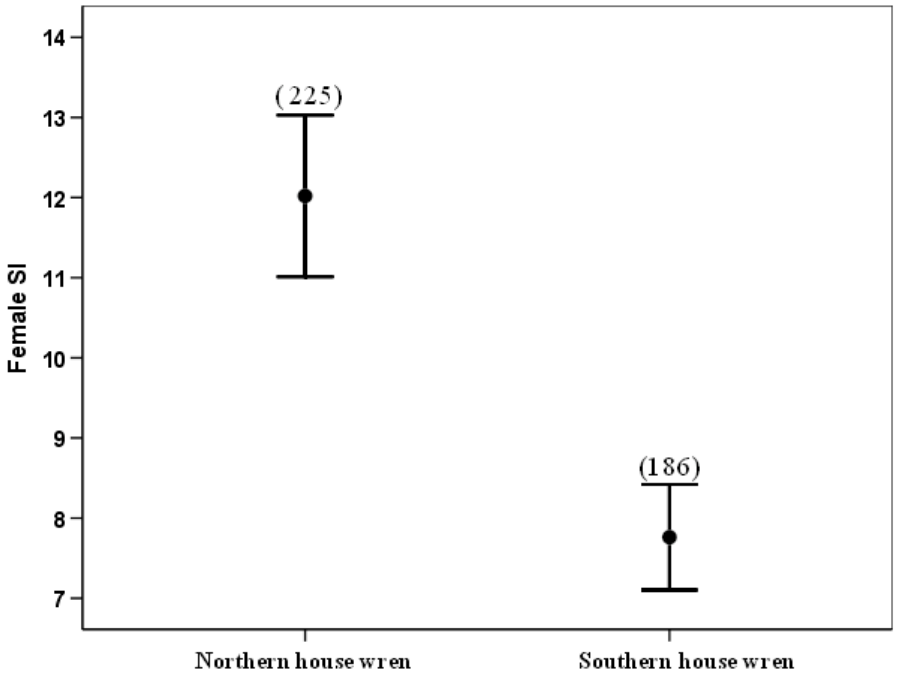

Figure 4.1: Mean female synchrony index (SI) for northern and southern house wrens. Sample sizes are given in parenthesis.

Early in the breeding season floaters occupied 62% of the 29 territorial vacancies that were filled in the southern house wren while in the northern house wren 22% of the nine replacements were floaters (X^2 = 4.37, P = 0.036; Figure 4.2). Late in the season, the proportions of replacements by floaters also were significantly higher in southern house wrens than in the northern house wrens (80% of 10 and 25% of 8 respectively, X^2 = 5.44, P = 0.003; Figure 4.2).

Female-female aggression experiments revealed that resident females were aggressive toward intruding females in both populations. Northern and southern house wrens did not differ significantly in the proportion of females that approached the simulated intruder when it was close to the primary box (82% N = 17 and 68% N = 28

respectively, $X^2 = 1.14$, $P = 0.286$) nor when it was installed close to the secondary box (33%, N = 9 and 38% respectively, N = 13, $X^2 = 0.06$, $P = 0.806$).

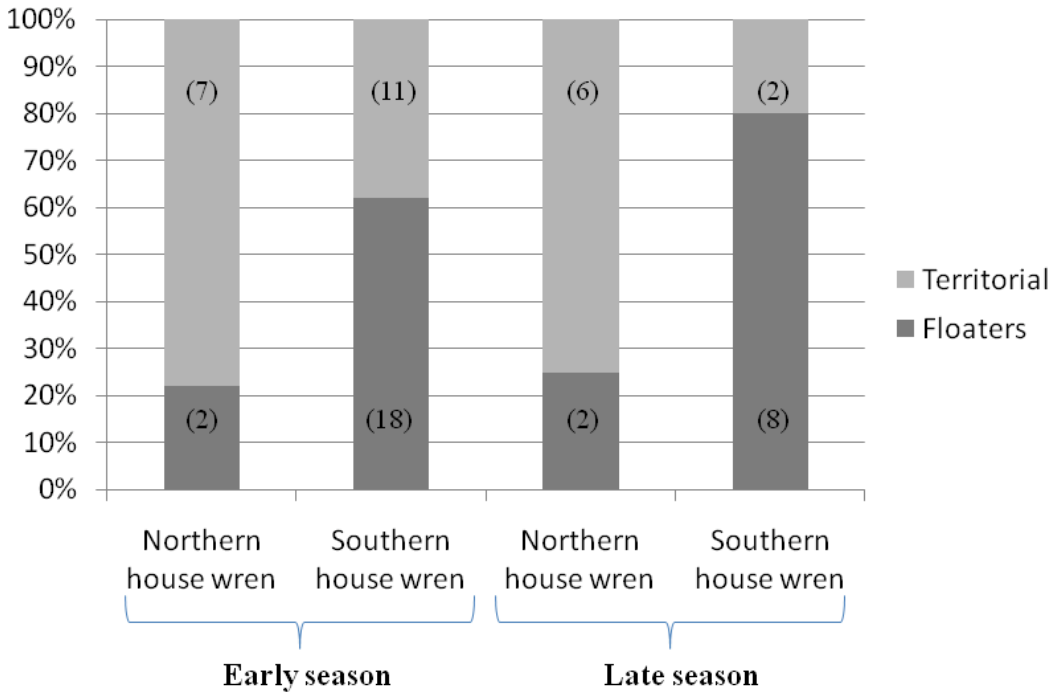

Figure 4.2: Composition of males occupying experimentally vacated territories in northern and southern house wrens. Sample sizes are given in parentheses.

When the simulated intruding female was set close the primary box, northern and southern house wren females attacked the cage in similar proportions (47% N = 17 and 43% N = 28 respectively, $X^2 = 0.08$, $P = 0.783$). However, when the intruding female was located close to the secondary box, the proportion of attacks was significantly higher for southern house wren females than for female northern house wrens (69% N = 15 and 27% N = 13 respectively, $X^2 = 4.07$, $P = 0.030$).

Nest-boxes did increase the quality of the territory, since the probability of monogamous pairs producing fledglings from nest-boxes in southern house wrens was higher than pairs breeding in natural cavities (0.62, N = 124 nests vs. 0.02, N = 63 nests,

respectively). Moreover, the probability of producing fledglings for a secondary female in a nest-box was 0.19 (N = 7 nests), which is higher than the probability of producing fledglings for a monogamous female in a natural cavity. However territory quality manipulation did not induce polygyny in the southern house wren. During 2004-2005, 83% of the pairs (10/12) which received two boxes in their territories switched from breeding in tree cavities to breeding in nest-boxes, indicating a strong preference for nest-boxes. None of these males attracted more than one female to their territories.

Territories of monogamous males were significantly larger for northern vs. southern house wrens ($X \pm$ SE = 1766.50 ± 136.09 m^2, N = 26 vs. 753.71 ± 51.257 m^2, N = 60, respectively; GLM, $F_{81} = 10.22$, $P = 0.002$), but territories of polygynous southern house wren males were of similar size to territories of monogamous northern house wren males ($X \pm$ = SE = 1511.36 ± 176.133 m^2, N = 9; GLM, $F_{29} = 2.40$, $P = 0.132$).

Discussion

Monogamy in the southern house wren seems to be maintained by both male-male competition and female-female aggression. The importance of the former is indicated by the male removal experiments, which revealed a greater prevalence of floater males in the southern than in the northern house wren (Figures 4.2), and by the fact that territories of monogamous males were smaller in the southern than in the northern house wren. Floaters are non-breeding males that will establish a territory and breed if territories and resources become available (Brown 1969). The greater prevalence of floaters in the southern population reflects more intense competition for breeding territories (Freed 1987), which can limit the opportunity of southern house wren males to monopolize more than one female. In a population where floaters are abundant, it should be difficult for a male to achieve breeding status by acquiring a territory, and even harder to acquire a territory large

enough to monopolize two females. Both northern and southern house wren males usurp territories by challenging and evicting the resident male (Freed 1986, Johnson and Kermott 1990), indicating that intrasexual competition is widespread in the species. A greater prevalence of floaters in southern house wren populations presumably results in greater male-male competition and an increase in the costs of monopolizing more than one female. When I removed males from the southern house wren population, polygyny increased briefly, but the population rapidly returned to low levels of polygyny, as all induced polygynous males eventually lost their secondary female either to floaters or unpaired neighbors.

Compounding the effects of male-male competition, female-female aggression prevents additional females that are attracted to a male's territory from settling down. Both northern and southern house wrens visited the caged female close to the primary and secondary box in similar proportions; hence detection of the intruding female did not differ between populations. Both northern and southern house wrens were aggressive to a simulated female intruder close to the nest, but a higher proportion of southern house wren females were aggressive when the caged female was installed near the secondary box. House wrens should be aggressive toward conspecifics close to the nest, since intruders normally take over nests by pecking eggs and killing nestlings (Freed 1986, Johnson and Kermott 1990). Slightly higher female aggression in the southern house wren might be related to the smaller size of territories, since a caged female anywhere on it can be a threat to the female's eggs or young. In contrast, a caged female on a larger northern house wren territory might be far enough from the nest of the resident female to avoid appearing threatening to her. Indeed, southern house wren polygynous males' territories were of similar size to northern house wren territories, suggesting that southern house wren males would need to monopolize large territories to become polygynous.

It has previously been shown that intrasexual competition is responsible for maintaining monogamy in other bird species. On Mandarte Island, Canada, song sparrow (*Melospiza melodia*) males are unable to defend a territory large enough to accommodate more than one female, and territorial females prevent the settlement of additional ones (Arcese 1989). Similarly, experiments with caged females by Sandell (1998) on European starlings (*Sturnus vulgaris*) and Slagsvold et al (1999) on pied flycatchers (*Ficedula hypoleuca*) suggested that female-female aggression can play an important role in preventing males from acquiring additional females. Hannon (1984) found that in the willow ptarmigan (*Lagopus lagopus*) male parental care is not essential and suggested that monogamy in this species is maintained by resident females preventing potential secondary females from settling. In brief, female-female aggression seems to be widespread in birds and might be an important factor in the prevalence of avian monogamy. Female aggression can be the result of females not tolerating intruding females who can potentially destroy the eggs or nestling and/or females attempting to ensure that male parental care is not shared with another brood. In the southern house wren, the first seems more plausible since males rarely abandon a primary female during the early stages of breeding to provide help for a secondary female.

The female breeding synchrony hypothesis (Emlen and Oring 1977) predicts that the social polygyny rate should be greater in populations where females breed asynchronously. Breeding asyhchrony should favor social polygyny in house wrens since males do not try to attract secondary females until the primary female starts incubation (Johnson and Kermott 1991). The data presented here do not support the asynchrony hypothesis since southern house wrens were far less likely to be polygynous even though the females in that population were less synchronous (Figure 4.1). However, in both populations some females bred asynchronously (Table 4.1), so both populations had the

potential to become polygynous. Thus, the female breeding synchrony hypothesis cannot explain the differences in polygyny rates between populations.

The territory quality manipulation experiment suggests that the male territory quality hypothesis, which predicts that increasing the quality of breeding sites should induce polygyny, is not enough to explain the maintenance of monogamy in the southern house wren. This result should be taken with caution, since I assumed that territory quality was determined by nest site quality although other variables such as food abundance, cover or territory size could be important. It has been suggested that for cavity nesters, variation in nesting sites might be more important than variation in food availability since it reduces nest predation (Orians 1961, Petit 1991, Pribil and Searcy 2001). Northern house wren females consider nest-boxes to be of higher quality than most natural cavities and might choose already mated males because they possess high quality nest sites in their territories (Johnson and Kermott 1993, Johnson et al. 1994). Supplying males with extra nest-boxes increases the polygyny rate of male northern house wrens in Wyoming, USA (Johnson and Kermott 1991) and in the otherwise monogamous prothonotary warbler (*Protonotaria citrea,* Petit 1991). Although southern house wrens' breeding success in nest-boxes was higher at my study site than in natural cavities and most females preferred to breed in nest-boxes (Llambías and Fernández 2009), the addition of nest-boxes did not induce polygyny. The reason extra nest-boxes induce polygyny in the northern house wrens, but not in the southern house wren, seems most likely to be related to the fact that southern house wren females are more aggressive toward intruding females close to the secondary box.

In summary, social monogamy in the southern house wren seems to be maintained by intrasexual competition. Male floaters are abundant in the southern house wren population leading to higher levels of male-male competition. Females are aggressive to each other indicating that females are territorial as well. Why might breeding habitat be more saturated with adults in the southern than in the northern house wren? Southern

house wrens at my study site in Argentina are residents and inhabit small forest patches surrounded by grasslands while northern house wrens in New York are migratory and breed along forest edges. Stutchbury and Morton (2001) proposed that for migratory birds, temporary breeding territories coupled with high overwinter mortality result in unoccupied areas for establishing territories during the breeding season. However, in resident birds with higher adult survival there should be a lower turnover in territories and greater competition for breeding sites (Freed 1987, Morton et al. 2000, Stutchbury and Morton 2008). I suggest that migration has important implications for the evolution of mating systems in house wrens and in other territorial passerines as well. In southern house wrens, enhanced adult survival and reduced territory availability result from the sedentary life style, and these reinforce social monogamy and increase the strength of intra-sexual competition. In northern house wrens, being migratory decreases adult survival and enhances territory turnover, decreasing intra-sexual competition. Future research on other bird species might help us to understand if the cascade of effects on social mating systems derived from being resident vs. migratory are widespread in birds.

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CHAPTER 5

FEMALE DISTRIBUTION AFFECTS THE SOCIAL MATING SYSTEM OF SOUTHERN HOUSE WRENS

Paulo E. Llambias

Abstract

A conventional view of avian mating systems is that females choose among males on the basis of the quality of males and their territories. Alternatively, it has been proposed that females compete for habitat and males compete to monopolize females. This alternative is based on the assumption that male breeding success depends on access to females while female breeding success depends on access to resources. By inducing polygyny and removing monogamous and bachelor territorial males in a resident population of southern house wrens (*Troglodytes aedon*), I evaluated several predictions of this male competition-female distribution hypothesis. If female distribution depends on territory quality but not on male distribution, experimentally widowed females should remain in their higher quality territories even in the presence of neighboring territories held by bachelor males. If male distribution is affected by female distribution, males should move into the territories of experimentally widowed females but not into vacated bachelor territories lacking females. Of 21 experimentally widowed females, 18 (86%) remained in their territories. Males either abandoned or expanded their territories to overlap with the widowed females. Eight males expanded their territories to breed polygynously and seven bachelor males (four from the study plot and three from nearby plots) abandoned their territories to move into the territories of experimentally widowed females. Most experimentally vacated bachelor territories remained empty for more

than a week, only 11% (1/9) of the territories were claimed by a floater. Polygynous males acquired two females' territories, thus defending significantly larger territories than those of monogamous males. Females mated to polygynous males did not overlap in area used while foraging, and their territories were of similar size to those of monogamous females. I suggest that in the southern house wren male distribution is limited by the territories of other males and female distribution is affected by the distribution of resources. Polygyny is not caused by a male attracting two females to his territory, as the conventional view proposes, but rather it occurs only when a male can effectively defend two distinct female territories because of the absence of competing males.

Introduction

Identifying the factors that affect male and female distribution is essential for understanding how ecological variables influence the evolution and maintenance of social mating systems. According to a conventional view of mating system formation in birds, males settle on breeding territories and then females choose among males (sexy son hypothesis, Weatherhead and Robertson 1979) and/or territories (polygyny threshold model, Verner and Willson 1966). Davies (1992) proposed the alternative view that females settle in relation to food and nest sites, and that males compete to monopolize female territories. This male competition-female distribution hypothesis proposes that in both migratory and resident populations, females use the same cues when making decisions on where to breed. However, migratory birds make settling decisions every breeding season, while sedentary birds might move between territories during the year, depending on new openings in the population. For migratory birds, where males arrive on the breeding grounds before the females, males should be

predicting the places where females will settle and thus what looks like female choice among males might actually be female choice of habitat (Davies 1991). For resident birds, males should adjust their distributions to overlap with females' distributions during any time of the year.

The male competition-female distribution hypothesis is based on the assumption that female breeding success is limited by access to resources (food availability and nesting sites) while male breeding success is limited by access to females. If this interpretation is true, then females should settle in relation to resources and males in relation to females. In brief, this hypothesis states that: 1) male distribution is affected by female distribution, 2) female distribution is affected by resource distribution, 3) females do not take into account male mating status, male quality, or the prospects of male help when settling on a breeding territory, and 4) females mated to a polygynous male do not share a territory, rather each female defends her own territory inside the polygynous male territory.

By inducing polygyny and removing monogamous and bachelor territorial males in a resident population of southern house wrens (*Troglodytes aedon bonariae*), I evaluated several predictions of the male competition-female distribution hypothesis. Specifically, I tested the following predictions: 1) if female distribution depends on territory quality but not on male distribution, induced widowed females should remain in their territories even in the presence of neighboring territories held by bachelor males, 2) if male distribution is affected by female distribution, males should move into widowed female' territories but not into vacant territories from which bachelor males were removed, and 3) polygyny can be induced, but only by two separate female territories becoming incorporated inside a male's territory. Additionally, I used previous published data on the migratory northern house wrens (*T. aedon aedon)* to

evaluate the prediction that females in the north base their mate choice on resource characteristics of male's territories, not on characteristics of the males themselves.

Methods

Study species

The house wren (*Troglodytes aedon*) is a sexually monomorphic, small (12g) territorial passerine that breeds in tree cavities or holes excavated by other bird species. The house wren ranges from Tierra del Fuego to Canada (Remsen et al. 2009), though some have suggested that the taxon be split into three species (Brummfield and Capparella 1996).

The present study was carried out in a population of southern house wrens (*Troglodytes aedon bonariae*) breeding in nest-boxes in Buenos Aires Province, Argentina. Southern house wrens are sedentary and remain in their territories year round (Freed 1987, Llambías and Fernández 2009). The predominant mating system is social monogamy, with distinct parental roles; females incubate and brood the nestlings and both sexes cooperate in building the nest and feeding the young (Brewer 2001, Llambías and Fernández 2009).

Field procedures

During October-January, 2004-2007, I studied southern house wrens breeding in nest-boxes in a cattle ranch (Los Zorzales), near the town of General Lavalle, Buenos Aires Province (36° 26'S, 56° 25'W), Argentina. Southern house wrens have been breeding in nest-boxes at the study site since 2003, when I erected two boxes per

male territory (N = 47 territories) in three forest fragments (total area 4.1 ha, box density = 23 boxes per ha). The forest fragments are mainly composed of *Celtis tala* trees (4-7m high) surrounded by pastures. Every other day, I visited territories to monitor the presence of color-banded individuals and check the nesting stage and breeding success of nests in boxes. I captured unbanded adults with mist nets or inside nest-boxes and assigned each individual a unique color-band combination. For detailed field procedures and study site description see Llambías and Fernández (2009).

Removal experiments

To test if male distribution is affected by female distribution I removed territorial males from the study site. During early October and before the onset of egg laying in 2004-2005, I captured 30 territorial males (9 bachelors, 21 monogamously mated) and released them 50km away in the botanical gardens of San Clemente del Tuyu. If a vacant territory was occupied by a floater immediately after removal, I captured and translocated the floater as well. As a result, immediately after the translocation, a proportion of females whose mates were removed were left unpaired in their territories, a proportion of bachelors' territories had no wrens, and several monogamous pairs and bachelor males were left in their territories (Table 5.1). All territories contained two nest-boxes.

Male removals during 2004-2005 induced polygyny in eight territorial males. To compare territory sizes of polygynous and monogamous males and of females mated to monogamous and polygynous males I incorporated two more polygynous males induced during 2007.

Table 5.1: Changes in territory availability after male removal experiments.

Territory Type	Number of territories 2004		Number of territories 2005	
	Before manipulation	After manipulation	Before manipulation	After manipulation
Widowed territories	0	28 % (13)	0	25% (8)
Vacated bachelor territories	0	9% (4)	0	16% (5)
Monogamous territories	85% (40)	57% (27)	69 % (22)	44%(14)
Bachelor territories	15% (7)	6% (3)	31%(10)	16% (5)

Female and male territories

During 2004, 2005, and 2007, I mapped territories of 21 females mated to monogamous males and 16 females mated to polygynous males using the minimum convex polygon (MCP, Mohr 1947, Odum and Kuenzler 1955, Barg et al. 2005). I excluded 5% of the locations furthest from the nest to avoid including spurious excursions and built a 95% MCP (Odum and Kuenzler 1955). To calculate the territory area I connected the outermost locations using the track function on a GPS (Garmin Vista HCx). I defined the core of the territory as the area surrounding the nest-box where the female bred and defined its boundaries by observing male and female for 20 minutes while foraging when nestlings were 2-3, 7-8, and 11-12 days old. Additionally, I used song playback to map male territories. I observed male's movements during two sessions of 15 minutes after stimulating aggressive behavior for five minutes. This was essential for mapping male territories because polygynous males did not feed the nestlings of the secondary female. To complete the polygon, I recorded the location of the adults during each nest check. All birds were followed between dawn and 1230 hrs EDT.

I compared territory size of monogamous and polygynous males and of females mated to monogamous or polygynous males with a general linear model (GLM) using social status and year as fixed factors. Statistical analyses were carried out in SPSS version 1.4 (SPSS 2005).

Results

Of the 21 experimentally widowed females, 18 (86%) remained in their territories. Of these 18, eight bred as secondary females with neighboring monogamous males who expanded their territories, and ten bred as monogamous females with territorial males or floaters who moved into their territories. The other three widowed females were not seen again at the study site, and are presumed to have abandoned the area.

Males either shifted or expanded their territories to overlap with the widowed females. During 2004-2005, eight males expanded their territories to breed polygynously and seven bachelor males (four from the study plot and three from nearby areas) abandoned their territories to move into an experimentally widowed female territory. Three vacancies were occupied by presumed floater males. Most vacated bachelor territories remained empty for more than a week, only one (11%) of these nine territories was claimed by a floater.

During 2003, 2004, and 2007, territories of females mated with polygynous males did not overlap and were of similar size to territories of females mated to monogamous males ($X \pm SE = 637.06 \pm 41.40 m^2$, $N = 16$ vs. $695.30 \pm 54.21 m^2$, $N = 21$ respectively; GLM, $F_{33} = 0.82$, Figure 5.1). Territories of bachelor males and monogamous males also were of similar size ($576.92 \pm 45.18 m^2$, $N = 20$ vs. $727.05 \pm 47.03 m^2$, $N = 68$, respectively; GLM, $F_{83} = 3.34$, $P = 0.071$, Figure 5.1). Territories of

polygynous males were significantly larger ($X \pm SE = 1511.36 \pm 176.13 m^2$, $N = 9$; GLM, $F_{71} = 27.90$, $P \leq 0.001$, Figure 5.1) than territories of monogamous males.

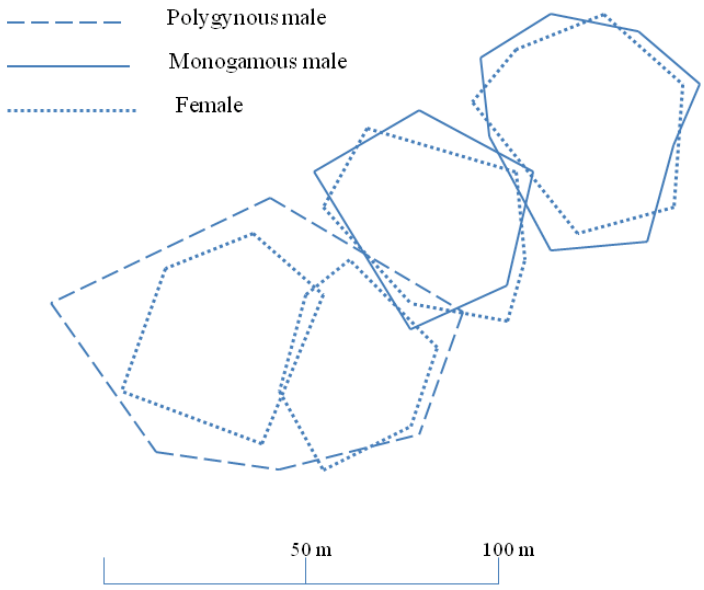

Figure 5.1: Territory of one of the experimentally induced polygynous males in 2004 along with the territories of the two nearest monogamous males in that year.

Discussion

In the resident southern house wren, males' distributions clearly are determined by female distributions. Results of male-removal experiments demonstrated that male southern house wrens adjusted their territories to overlap with female distributions: (1) males abandoned their territories and moved into territories of experimentally widowed females, (2) neighboring monogamous males expanded their territories to incorporate territories of experimentally widowed females, and (3) former bachelor territories that were experimentally emptied remained vacant for more than five days. Although bachelor males existed in the study plot, females did not move to join these bachelors, suggesting that female distribution did not respond directly to

male distribution. During 2003-2007, the bachelors' territories with induced vacancies were used as breeding sites by house wrens, so it is not likely that these areas were unattractive to females. Indirect evidence gives further support to the prediction that female distribution was driven by resource distribution at my study site. Nest-boxes are generally better nest sites than natural cavities, and occasionally some females breeding in territories without boxes abandoned their males and territories to pair with a male with a nest-box in his territory (Llambías and Fernández 2009). A lower proportion of bachelor males occurred in plots provided with nest-boxes compared with plots where wrens bred only in tree cavities (Llambías and Fernández 2009). Still, it cannot be concluded that male quality is not important for female's settlement decisions, since higher quality males might defend higher quality territories with nest-boxes. Future research should include experimental designs that decouple the quality of males and their territories.

In the migratory northern house wren, female distribution also appears to be determined by resource distribution rather than male distribution. Johnson and Searcy (1993) assigned two types of nest-boxes to already mated males to which they could attempt to attract a secondary female: standard-type nest-boxes with small entrance holes in the front of the box versus boxes with larger entrance holes located in the roof. Females more frequently chose mated males with standard-type nest-boxes, suggesting mate choice based on characteristics of the nest site, not the characteristics of the male himself. Furthermore, at a different study site, manipulation of abundance of nest-boxes on territories after males had settled but before females had arrived to the breeding grounds showed that male time-to-pairing was independent of male condition index or vegetation characteristics in the territory, and negatively related to the number of potential nest sites on a male's territory (Eckerle and Thompson 2006). As in the southern house wren, northern house wren females prefer to mate with males

that control nest-boxes rather than natural cavities. Johnson and Kermott (1991) observed higher levels of polygyny in northern house wrens breeding in nest-boxes than in natural situations where males only had access to tree cavities. Finally, Johnson et al. (1994) proposed that northern house wren females breeding in nest-boxes choose already mated males because these males possess high-quality nest sites. Access to nest-boxes would provide females with compensation for the cost of polygyny under normal conditions when all available unmated males would have lower quality nest-sites. This hypothesis suggests that northern house wren females choose nesting sites rather than males when making decisions of where to breed. Northern house wren females frequently engage in extra-pair copulations (Soukup and Thompson 1996, Soukup and Thompson 1997), suggesting that females might prefer a different male to sire some of her offspring than the one that holds the territory. In brief, my results from the sedentary southern house wren in Argentina together with published data on the migratory northern house wren in the US provides strong evidence for the male competition-female distribution hypothesis.

Polygynous southern house wren males had bigger territories than monogamous males because they expanded their territories to overlap with two females' territories. This kind of polygynous mating system has been termed "sublease territory" by Gould and Gould (1989) and is a particular case of resource-defense polygyny (Cézilly and Danchin 2008). Sublease territorial polygyny is not well documented in birds, perhaps because much more effort has gone into describing male territoriality. It has been shown in the song sparrow (*Melospiza melodia,* Arcese 1989) and dunnoks (*Prunella modularis*, Davies 1992) that females mated to polygynous males overlap little in the areas used. Female territoriality has not been studied in the northern house wren, but Johnson (1998) reported that "Primary and secondary females rarely if ever interact" suggesting that both of them have independent

territories. Ford (1991) defined polyterritorial polygyny as polygyny where males hold two or more disjunct territories and attract a single female to each of them. He reported that 11 species of North American passerines and 17 species of European passerines are sometimes polyterritorial. Polytorritorial polygyny can be viewed as a particular case of sublease territorial polygyny, in which females' territories are not adjacent. Sublease territorial polygyny might be more frequent in passerines that it has been assumed. Furthermore, in several species it has been observed that males became polygynous by expanding their territories and incorporating a second female (seaside sparrows, *Ammodramus maritimus*, Greenlaw and Post 1985; dunnocks, Davies 1992; song sparrows, Smith et al. 1982; tropical house wrens, Freed 1986). Further support that male distribution is affected by female distribution is given by removal experiments in migratory Black-throated blue warblers (*Dendroica caerulescens*, Marra and Holmes 1997) and in the resident superb fairy wren (*Malurus cyaneus*, Pruett-Jones and Lewis 1990), where new or neighboring males moved to territories that were occupied by females but not to territories without females.

If in birds male distribution does not affect female distribution, then female selection of the social mate and of the mate who will sire her offspring can be decoupled. Females might first choose a territory for breeding, then form a pair-bond with the owner of that territory to increase the security of her occupation of the space. Perhaps only later she chooses one or more mates to sire her offspring. Females should allow the owner of the territory to sire at least some nestlings, since males might withold help in raising the brood or expel the female from the territory if unable to fertilize some of the eggs. Extra-pair fertilizations are widespread even though most bids are socially monogamous (Sherman 1981, Westneat and Sherman 1990, Westneat and Stewart 2003). Decoupled female choice would explain this pattern. In the migratory white-crowned sparrows (*Zonotorchia leucophrys*) at Tioga Pass,

California, females often make their breeding site choices before male arrivals (Westneat et al 1990). Females settle in the same territories where they have bred successfully the previous year, regardless of the presence of their former mate, and seek extra-pair copulations if the new mate is young and inexperienced (Sherman and Morton 1988, Westneat et al. 1990). In the white-crowned sparrow, female choice is decoupled, since they first choose a site to breed and later the male who will sire their offspring.

The male competition-female distribution hypothesis proposes that the conventional view that females choose among male territories and assesses male status might be wrong, and suggests instead that females compete for habitat and males compete to monopolize females. Future research with an experimental design involving the separate manipulation of territory and male quality and removal of females will do much to further illuminate mating systems in house wrens in both hemispheres. Similar work in other species could test the general applicability of a male competition-female resource view of avian mating systems.

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